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Infant Colour Perception

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Declaration

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Signature:

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Article Format Thesis Declaration

The thesis conforms to an 'article format' in which the first chapter presents an overview of the relevant literature, an outline of the empirical work of the thesis, and discussion of the overall contribution of the thesis to the field. The remaining four chapters consist of discrete papers written for publication in peer-reviewed journals. One of these chapters has been published, two have been submitted for review, and one is prepared for submission.

Chapters and Author Contributions

Chapter 1 provides an introduction to the relevant literature, along with an outline of the empirical work of the thesis, and a discussion of the main findings, implications and conclusions

Chapter 2 is published in the *Proceedings of the National Academy of Sciences* as :-

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<u>UNIVERSITY OF SUSSEX</u>

<u>ALICE ELIZABETH SKELTON – PHD PSYCHOLOGY</u>

<u>INFANT COLOUR PERCEPTION</u>

<u>SUMMARY</u>

We have learnt a lot about the development and maturation of colour vision in infants, but know comparatively little about the development and structure of colour perception once trichromacy has been established. This thesis aims to characterize infant colour perception in the first year of life over several areas which have previously been well documented in adults; colour categorisation, colour preference, perception of illusions, and infant sensitivity to natural scene statistics.

Paper 1 (Skelton, Catchpole, Abbott, Bosten, and Franklin, 2017) systematically mapped infant colour categories revealing that infant colour categories are related to the retinogeniculate pathways of colour vision. Paper 1 also illustrates and quantifies the correspondence between infant colour categories and commonalities found across the worlds' colour lexicon. Paper 2 shows that infants look for longer at the colours which adults prefer, and provides evidence for an influence of low-level mechanisms on infant response to colour and adult preference. Paper 3 (under review) reopens the question perception of the Munker-White illusion in infants aged 4 to 8 months, through the replication of a previous study and the use of an alternative method, with discussion of the reasons for studying illusions in infancy. Finally, paper 4 provides the first substantive evidence that infants aged 4 months are sensitive to natural scene statistics, as evidenced though the presence of a blue-yellow discrimination bias commonly associated with the distribution of chromaticities found in natural scenes. Paper 4 also has critical implications for the use of psychophysical methods in infants and adults.

The findings inform our understanding of infant colour perception and general perceptual processes by outlining some of the structure around which infants' colour perception is built. The early structure of infants' perception of colour is shown to often have commonalities with adult colour perception.

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Chapter 1 - Introduction & Thesis Overview

The phenomenon of colour has extensively captured the interest of people from a wide range of disciplines. Philosophers have long used colour in thought experiments (see Hume's missing shade of blue (Morreall, 1982) or 'Mary's room', (Jackson, 1986)) to debate concepts such as qualia . Anthropologists and linguists take interest in how the way we speak about colour has grown and evolved over time in response to our environment or culture (e.g. Hovers, Ilani, Bar-Yosef, & Vandermeersch, 2003; Lucy, 1997; Thavapalan, Stenger, & Snow, 2016). Artists manipulate colour to provoke specific feelings that would otherwise be difficult to capture (see Finlay, 2014 for a review), and architects use colour as more than just decoration, using it to shape our perception and response to physical space (e.g. Dalke et al., 2006). In the field of Psychology and Cognitive Science, colour's ability to be tightly controlled and defined in terms of low level sensory inputs makes it the ideal stimulus for exploring a range of topics in perception and cognition. Colour has been used to study topics including attention, salience, visual aesthetics, and categorisation (Elliot, Fairchild, & Franklin, 2015). The investigation of colour can also help researchers understand more about the structure and constraints of the visual and neural system (e.g. Conway, 2009), and how experience may interact with these 'built in' processes to shape our perception of the world (e.g., Wachtler, Doi, Lee, & Sejnowski, 2007).

The apparent dichotomy between colour as a shared physiological response and as a seemingly very personal perceptual experience makes it an ideal and fascinating tool for studying human perception, cognition and behaviour. Most people would

prefer to have colour vision than to not have it, but despite colour being a large and enjoyable part of our perceptual experience and the wealth of studies on adult colour perception, there are many elements of colour perception where there still remains lively debate. For example; there remain questions on the origins of colour categories, how colour perception is shaped by experience and what mechanisms underlie our experience of colour. A developmental approach can provide critical insight into these exciting questions in the field of colour science. Over the first few months of life the infant visual system undergoes a large maturational change, whilst simultaneously undergoing changes in the quality and quantity of perceptual experience. As a result, the early months of life are an ideal place to investigate questions on both the commonalities in our perceptual experience as adults, and the underlying structure of our colour perception.

This thesis presents an investigation of multiple aspects of colour perception and cognition in human infants. The goals of the thesis are to: (i) progress our understanding of human processing and experience of colour in both infants and adults; (ii) to further understanding of infant perception and cognition; and (iii) to address broader fundamental debates in the cognitive sciences. In order to fully understand the motivations of the studies of this thesis and how they are situated in a broader context, this Introduction and Overview section first reviews the relevant literature: it provides a brief introduction to the physiology of colour and colour models along with brief discussion of some areas of interest in the field of colour science. Following this, there is a discussion of the development of colour vision, and an overview of our current understanding of infant perception both in

colour and other domains.

1.1.   The physiological basis of colour

Newton's renowned prism experiments in 1672 (reported in Newton, 1972) were one of the greatest advancements of our scientific understanding of colour, being the first to clearly define colour in terms of wavelengths which are fixed in a set order (the colour spectrum). Since then, there has been a great deal of research on the physiology of colour vision. We now know that humans have three independent receptor types which are sensitive to colour (a concept proposed by Young, (1802) and which is now known as 'trichromacy'). These photo-pigments are known colloquially as 'red', 'green', and 'blue' cones due to the regions in the colour spectrum where their peak sensitivity lies, but each cone is sensitive to a specific *range* of wavelengths of light; short (S cones), medium (M cones), and long (L cones).

The relative strength of the wavelengths detected are compared in order for the brain to 'see' visible light in a process known as cone-opponency. The origin of cone-opponent theory derives from Hering's (1874) observations that there are four unique chromatic experiences: blue, red, green, and yellow, and that there were patterns in the relationships of these unique sensations (e.g. blue-green is a real possible colour, but blue-yellow is not). Physiologically this is represented early in the visual system by three separate channels in the retinal ganglion cells, two which give us the 'cardinal directions' of colour (reddish-greenish and blueish-yellowish) and the third for luminance (De Valois, Abramov, & Jacobs, 1966;

Derrington, Krauskopf, & Lennie, 1984; Krauskopf, Williams, & Heeley, 1982). Cone

opponency reduces the amount of redundant information generated by overlap

between the cones' spectral sensitivities, and also reflects the properties of the

spectral properties found in natural scenes (Lee, Wachtler, & Sejnowski, 2002).

This suggests that some elements of the visual system may have developed over

the course of evolution or in early life, as a result of interactions within our

environment (see also Wachtler, Doi, Lee, & Sejnowski (2007) for discussion on the

relationship between natural scenes and cone-specific statistical learning).

1.2.   Colour in the Cortex

Rather than there being one central area in the cortex responsible for

processing colour, colour perception appears to be distributed across a network or

regions (Gegenfurtner, 2003, Solomon & Lennie, 2007). Earlier regions of the

visual cortex predominantly process wavelength information, whilst later regions

appear more specialised for shaping our final perception of colour. For example,

cells in V1 respond to the wavelength of light being reflected from an object, while

cells in V4 appear to discount the information about the illumination which is

embedded in these wavelengths, responding instead to the surface colour of the

object we are looking at (Shipp & Zeki, 1985; Wild, Butler, Carden, & Kulikowski,

1985). This helps us to continue perceiving an object as being a constant colour

despite changes in the reflected wavelength from the object as a result of changes

in the illumination, a process known as colour constancy. Differences in cell

selectivity alone cannot account for the entirety of colour constancy, and there

remains much to understand about its cortical mechanisms. For example, there is debate about the role and time course of statistical learning from natural scenes on the mechanisms of colour constancy at the cortical level (Cecchi, Rao, Xiao, & Kaplan, 2010; Pearce, Crichton, Mackiewicz, Finlayson, & Hurlbert, 2014).

Single cell recordings in macaques have revealed 'colour maps' of hue selective regions stable across different levels of cortex (V1, Xiao, Casti, Xiao, & Kaplan, 2007; V2, Wang, Xiao, & Felleman, 2007; and V4, Tanigawa, Lu, & Row, 2010). Similar hue maps have not yet been reported in humans due to limitations in achieving the necessary resolution in order to do this, although given similarities in the processing of colour in humans and macaques it may be expected that similar hue maps would be found in humans. fMRI studies of humans have shown that populations of neurons in V1 and V2 of the visual cortex show a colour opponent response (Engel, Zhang, & Wandell, 1997). However, cells in the LGN tend to cluster around the cardinal directions of colour, whilst those in the cortex (V1, V2, V3 and V4) selectively respond to intermediate hues, as well as the opponent cardinal axes, (Gegenfurtner, 2003; Kuriki, Sun, Ueno, Tanaka, & Cheng, 2015).

Many cells which respond to colour also appear to respond to other aspects of object perception such as shape, or texture (Grill-Spector et al., 1998; Lennie, Krauskopf, & Sclar, 1990; Zeki & Marini, 1998), although in mid-regions specialised for more complex scenes there is evidence of separate processing channels for colour, shape, and texture (Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010). A more recent study has attempted to parse these processes of where the in the cortex low level sensory input about wavelength becomes 'bound' to an object

surface, and suggests that these processes converge around V2 (Seymour, Williams, & Rich, 2016). This coincides with the presence of 'glob' and 'interglob' cells found in V2 (Conway, 2009) which respond predominantly to colour, although some are often also orientation selective. Globs have been shown to have luminance independent tuning to colour, and appear to be responsive to both hue and saturation dimensions of colour (Stoughton & Conway, 2008). Interglob cells in comparison do not respond independently to luminance (Conway, 2009), and are more likely to be orientation tuned than globs.

There is some debate as to the extent that colour signals converge with the processing of other features of objects such as shape. There is, for example, evidence of an input of signals from the S-cones into non-colour selective regions such as the MT (a region of the brain which processes motion) but there are behavioural differences in the processing of shape and colour suggesting a dissociation between the two processes (Conway, 2014). Colour is used in object recognition, evidenced partly by the dominance of the ventral stream in the processing of colour (Ungerleider & Haxby, 1994). Currently it appears that anterior regions of the ventral visual processing system show an interaction between colour and shape processing (Simmons et al., 2007), whilst posterior regions are shown to process these features separately (Conway 2014). This highlights that there is a difference between colour processing from cells which are colour *selective* or those which are colour *sensitive*. Whilst some cells are able to represent the composition of a selective hue, other cells instead may be sensitive to the fact that there is a hue there regardless of what that hue is. This is thought to be beneficial for object processing, as cells found in object processing regions can

encode the presence of a hue boundary (Conway, 2009).

1.3.   Models of Colour

Early colour science is dominated by 'simple' linear representations of colour, (e.g. Aristotle represented colour as a ratio of the brightest to darkest components of the object being seen, Barnes, 2014). Robert Grosseteste in the 13th Century was one of the first to describe colour using a more complex continuous and combinatorial 3D space (Smithson et al., 2012), more similar to the chromaticity diagrams used today. Rigorous physiological and psychophysical testing means that we now have models of colour which allow for accurate rendering of stimuli across studies, as well as measured control of stimuli across colour dimensions (e.g. saturation, lightness). Colour models commonly are either tied to the physiology of colour vision alone, or are developed with the aim of being structured along perceptual dimensions of colour and of being perceptually uniform (figure 1.1). Here, a selection of colour models are discussed which are relevant to the current thesis.

The MacLeod Boynton Chromaticity diagram (MacLeod & Boynton, 1979) is an example of a representation of colour tied to the physiology of colour vision. In the MacLeod Boynton chromaticity diagram, the Cartesian axes represent the early mechanisms of colour by giving the relative cone excitation of the L, M, and S cones in a single luminance plane relative to the central (origin) adaptation point. The horizontal axis allows for variation between L and M cones whilst keeping the input of S cones constant, and the vertical axis varies the response of the S cone.

The vertical axis is often referred to as indicating changes along the "blueish-yellowish" direction, however, it is the negative diagonal (from upper left to lower right on figure 1.1a) which shows the location of the true "blue-yellow" axis.
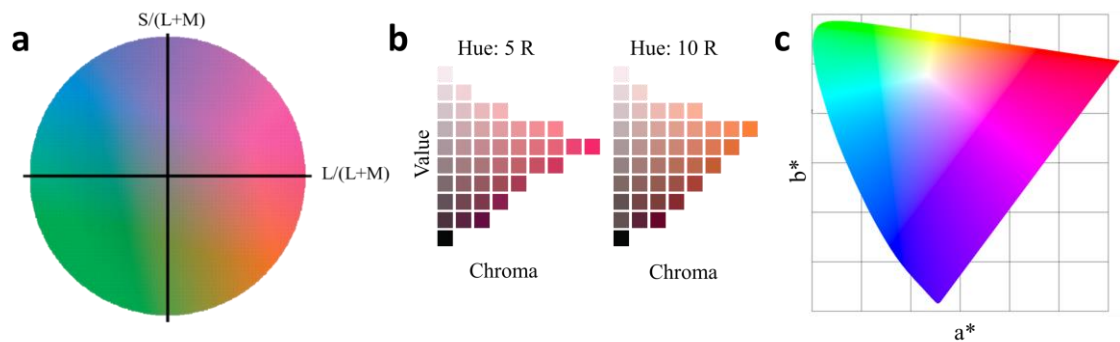
Figure 1.1. Representations of different colour models, due to differences in display monitors and printers. Colours are representative only, and not necessarily colorimetrically accurate. a) The MacLeod Boynton chromaticity diagram, showing the 'cardinal directions' of blueish-yellowish and reddish-greenish as determined by the relative excitation of cones in early colour mechanisms, b) an example of two hues (5R and 10R) from Munsell colour system, designed to be perceptually uniform within the dimensions of hue, value (lightness), and chroma ('colourfulness', roughly equivalent to saturation). Note in particular that the maximum chroma possible is not equal across hues, and c) CIELAB (1976), shown in the figure is a single lightness level, the horizontal axis represents changes in red-green, and the vertical axis changes in blue-yellow.

Discrimination across the colour spectrum is not equal (see e.g. MacAdam, 1943):
in some regions of colour space a larger difference is needed between a colour and
a reference in order to be discriminated than in others. Several models of colour,
such as the Munsell colour system (Cleland, 1921) and CIELAB (Commission
internationale de l'éclairage ,1976), aim to present colours in perceptually uniform
spaces. The Munsell colour system specifies colour along three dimensions; hue,
value (lightness), and chroma (similar to saturation, or 'colourfulness'), and aims
to equate stimuli so that each step along each of these hue dimensions is
perceptually equivalent. Munsell card is commonly used to present physical
surfaces to participants, and aims to be representative of typical colours in natural
scenes (providing it is viewed under a standard illuminant C). CIELAB in
comparison is designed to be a perceptually uniform representation of the cone-
opponent mechanisms, varying in luminance (L*), red-green (a*), and blue-yellow
(b*). All colours in CIELAB are defined relative to a white point, and so knowing
the white point of a stimulus set (usually defined as the background colour on
which stimuli are presented) is necessary in order to reproduce those colours with
accuracy.

1.4.   Colour: Perception, Cognition and Behaviour

Colour affects our perception, cognition and behaviour in many ways. In a
typical day our interactions with colour may involve: using colour information to
help us to visually search for objects, to communicate effectively and efficiently
about objects, our surroundings, or even our emotions (consider colloquial

phrases such as 'seeing red', 'green with envy'). We also use colour information when making judgements about an object both practically (as in judging the ripeness of some fruit) and aesthetically. Here we discuss a brief selection of the topics which investigate colour perception and cognition.

One topic that has received a lot of attention is that of colour naming. Whilst humans have the ability to discriminate millions of colours (Kaiser & Boynton, 1996), the colour continuum is grouped by colour terms into discrete categories such as red, green, blue etc. Broadly speaking, categorisation is a domain general process which allows for more efficient processing of our sensory experience. A further advantage of categorisation of colour is that it allows us to communicate more effectively about the colours and objects in our environment (Gibson et al, 2017). The number of colour categories in adult colour lexicons varies across languages (Kay, Berlin, Maffi, Merrifield, & Cook, 2009), but commonalities across languages indicate that this variation is not solely culturally defined (Jraissati & Douven, 2017; Kay & Regier, 2003; Regier, Kay, & Khetarpal, 2007). Further evidence for processes prior to cultural influence is the well documented phenomena of pre-linguistic infant colour categories (see for example, Bornstein, Kessen, & Weiskopf, 1976; Franklin & Davies, 2004; Yang, Kanazawa, Yamaguchi, & Kuriki, 2016).

There is much debate on whether how we speak about colour influences our perception of it (Regier & Kay, 2009). It has been argued that pairs of colours are easier to distinguish on certain tasks if they are from different lexical categories than if they are both from the same category (Daoutis, Pilling, & Davies, 2006; Kay & Kempton, 1984; Drivonikou et al., 2007, although see Wright, Davies, & Franklin,

2015 for discussion on the reliability of these effects). There remains debate around to what extent these categorical colour effects are due to early sensory processes or perceptual warping, or due to the effect that colour terms have on attentional, top-down or post-perceptual processes (Clifford, Holmes, Davies, & Franklin, 2010; He, Witzel, Forder, Clifford, & Franklin, 2014).

Another topic that has received much attention is that of the role of colour in visual search. Visual search tasks have revealed colour to be a particularly salient feature in our perception (Turatto & Galfano, 2000). When scanning a scene, attentional processing is often drawn to colour. This can happen via two mechanisms, widely defined as being either 'top-down' or 'bottom-up'. Top-down mechanisms can include broad relational judgements of the stimulus ('bluer', 'redder'), as well as more focused feature processing, where all stimuli which provide a feature match to the target stimulus receive a 'signal boost' and attract further processing (Schönhammer, Becker, & Kerzel, 2017). Colour can also capture attention even when colour features are task-irrelevant by utilising bottom-up mechanisms responsive to salience and contrast (Hickey, Mcdonald, & Theeuwes, 2006; Theeuwes, Reimann, & Mortier, 2006). Psychophysical evidence shows that stimuli which capture our visual attention via these low-level bottom-up mechanisms do not necessarily always result in visual awareness. In one eye-tracking task where participants had to report the colour targets which they fixated, participants often fixated coloured targets which they do not report as having seen, showing the disconnect between visual attention and visual awareness (Etchebehere, Fedorovskaya, 2017; Lamme, 2003).

The top-down and bottom-up mechanisms of attention to colour, although

separate, are not entirely independent. Predictive models of salience and colour

show that the salience of colour can vary according to the scene being viewed

(Frey, Honey, & Konig, 2008). Reds and greens appear particularly salient when

viewing a rainforest scene, in comparison to all colours in fractal pattern being

equally salient. This highlights an interaction between top-down and bottom-up

mechanisms during colour perception, as low level sensory processes alone are

shown not to be solely responsible for looking behaviour in adults. Other studies

have also shown that higher level perceptual processes can modulate colour

perception. For example, participants' memory of an object's colour will influence

their perception of an achromatic version of that object. When asked to adjust an

image of fruit until achromatic participants will often 'over shoot' the greyscale

point, in order to counteract their perception of the fruit still being coloured. A

greyscale image of a banana will still appear slightly yellow to participants, and so

the hue will be adjusted to appear more blue-ish to reach a point they perceive it

as being achromatic (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006)

A third topic in the investigation of colour perception and cognition is the

investigation of the potentially more 'personal' behavioural responses to colour

such as colour preference, colour emotion associations, and cross modal responses

to colour. Studies of colour preference and colour associations can tell us a great

deal about how information across the senses is integrated and associated as

seemingly unrelated sensations become bound together in a non-trivial manner.

Much research has pointed out the similarities in colour preferences across

participants despite people feeling that their preference for colour is an

idiosyncratic phenomenon (Hurlbert & Ling, 2007; Palmer, Schloss, & Sammartino, 2011). There are several theories about the origins of these preferences, many relating to affective experience with objects in the environment over the course of a life span or evolution (Humphrey, 1976; Palmer & Schloss, 2010), and others suggesting an influence of biological mechanisms on colour preference (Hurlbert & Ling, 2007).

There have also been studies which report an association between colour and emotion. Highly saturated yellows and oranges are more commonly associated with happiness than desaturated blues and greys, which are usually associated with sadness (Palmer, Schloss, Xu, & Prado-león, 2013). There is a suggestion that these emotions could also mediate other cross-modal correspondences such as those found between music-colour (Palmer et al., 2013), and smell-colour associations (Schifferstein & Tanudjaja, 2004; Dematte, Sanabria, & Spence, 2006), with 'nice' smells and up tempo music being associated with colours commonly associated with happiness. However, there remains debate as to what the exact mechanisms behind these emotionally mediated correspondences would be, with some suggesting that these become linked only once there is a semantic relationship between the two sensory processes ('semantic mediation'). There are other forms of cross-modal associations with colour which do not relate to a mediating factor of emotion, such as between colour and touch (Ludwig & Simner, 2013). This has led to suggestions either that there may be commonalities inherent in the processing of the separate stimuli themselves, such as a similar firing pattern in the early sensory processing of stimuli, or that co-occurrence in early

perceptual experience may lead to the re-enforcement of neuronal pathways which persist across the life span (Spence, 2011; Spence & Deroy, 2013).

Many who use colour in a creative context manipulate their use of colour to communicate a particular meaning or emotion (see Finlay, 2014 for a review of the historical use of colour in art) often with the aim of creating something aesthetically pleasing. Experimentally it's been shown that viewers' prefer the colours used in art to differ from the distribution of chromaticities commonly found in natural scenes. When asked to adjust the colours in unfamiliar paintings (both abstract and figurative) to what they think is subjectively the most attractive, participants choose colours close to the original composition of the painting. The original composition of these images is also the point where the colours in the image share differ from the distribution of chromaticities found in natural scenes (Nascimento et al., 2017). Although we may not consciously be aware of the distribution of chromaticities in natural scenes, we do appear to have a sensitivity for them demonstrating how our experience (evolutionarily, or over the course of a life-time) may influence our aesthetic appreciation and response to stimuli in the environment.

1.5.   Interim summary and outstanding questions on colour perception

This brief summary of some of the topics in colour science demonstrates the complex and diverse range of questions and debates of the field. Many of these colour phenomena are embedded in our daily experience to the extent that we often take them for granted. Broadly, studies of colour fall into two central but

intertwined questions, firstly, what are the physiological mechanisms behind our processing of wavelengths, and secondly, what processes determine our actual perception of colour? This thesis is primarily concerned with the second question, and focuses specifically on colour perception at its roots, in early infancy.

Adult studies alone cannot explain transitions in development or how the maturing visual system interacts with the role of perceptual experience. As such, studies of infant colour perception are valuable to help researchers understand how the world appears to the developing infant, as well as the origins of adult colour perception. Understanding the mechanisms of colour perception in infancy can also further our understanding of perceptual learning more broadly both in infancy and across the developmental life span (Yermolayeva & Rakison, 2014). Several central questions and studies in colour science have highlighted that experience can shape our colour perception, and whilst infants are not completely inexperienced in the world, they are by no means adult-like in the quality and quantity of their experience. Additionally, commonalities found in our perception of colour across individuals point towards underlying mechanisms which may be built upon across development. Studying infant colour perception provides an opportunity to examine both the underlying mechanisms of our visual perception, and how these may be modulated by experience and culture.

1.6.   Infant Colour Vision

As the visual system matures in the first few years it undergoes many anatomical changes. At one week post-natal infants' cones have become more

elongated than they were prenatally. The density of the cones in the fovea increase

rapidly postnatally, with cells also migrating from the central fovea to the

periphery (Hendrickson, 1994; Yuodelis & Hendrickson, 1986). Foveal density and

elongation of the cones continues to happen across the first five years of life, whilst

the cell migration and subsequent formation of the foveal pit completes at 15

months old (Barbur & Rodriguez-carmona, 2014; Yuodelis & Hendrickson, 1986).

Colour vision in very early infancy appears to be mediated through sub-cortical

pathways (Atkinson, 1984; Nardini, 2017). Whilst it has been shown that the

magnocellular pathway (primarily responsible for processing luminance and

motion) is functional at birth, the parvocellular pathway (usually implicated in the

processing of colour) is not (Hammarrenger et al., 2003). The magnocellular

pathway also develops much faster than the parvocellular pathway, suggesting a

dissociation between these two pathways in early infancy. At 4-months however,

infant contrast sensitivity functions (used as a measure of underlying parvo and

magno-pathway function in adults) show a similar pattern to those found in adults

(Dobkins, Anderson, & Lia, 1999). Although development of the parvocellular

pathway is slower than magnocellular development, there is still a significant

amount of development within the first few post-natal months. Colour vision

matures alongside the improvement of more general cortical information

processing (Grieve, Emerson, Fifer, Isler, & Stark, 2003; Nardini, 2017), which

includes a peak in synaptogenesis in the primary visual cortex at about 4-months-

old (Huttenlocher, 1990). There is evidence from children that higher order

association cortical processes only mature after the maturation of lower-level

somatosensory and the visual cortices (Gogtay et al., 2004).

Although possessing a less mature visual system than adults, infants do have some, albeit limited colour vision at birth, and even new-born infants' pattern of response to coloured stimuli is measurable and predictable. Studies of new-born infants demonstrate that they will look preferentially at a chromatic stimulus, rather than an achromatic stimulus, when that chromatic stimulus is of a long wavelength (red, green) and the stimulus is large (Adams, 1989; Adams & Courage, 1995; Teller, Peeples, & Sekel, 1978). Infants respond equivalently to achromatic and short wavelength (blue) chromatic stimuli at birth, and first show evidence of discrimination of short wavelengths around two months of age (Brown & Teller, 1989; Zemach & Teller, 2007).

Infant chromatic discrimination thresholds are larger than those of children and adults (Knoblauch, Vital-Durand, & Barbur, 2001; Zemach & Teller, 2007). However, the improvement of discrimination thresholds along the protan (L cone), deutan (M cone), and tritan (S cone) dimensions of colour vision is very rapid, decreasing by a factor of 2 with each doubling of age as measured from 4 months old (Knoblauch et al., 2001). Thresholds along the protan, deutan, and tritan axes show a similar pattern of improvement, although improvements along the tritan axis are slightly slower, and tritan discrimination thresholds remain larger across the lifespan. Although discrimination thresholds may be larger, the ratio of discrimination thresholds along of the protan, deutan, and tritan axes are similar in infancy to those found in adolescents and adults.

Although the component parts of colour vison may be operational in infancy, this alone does not guarantee infants are trichromatic in the same way as adults. However, many studies have confirmed that young infants (aged 2 months) are

able to make discriminations which adult dichromats cannot (e.g. Bornstein, 1976;

Suttle, Banks, & Graf, 2002). In order to confirm if infants were trichromats, Brown

& Teller (1989) measured the spectral sensitivity of 2-month-old infants and found

that infants showed a dip in sensitivity around 570nm which is also found in adult

trichromats. This point, commonly referred to as a 'Sloan notch', is the result of the

structure of the cone opponent mechanisms underlying human trichromacy

(Thornton & Pugh, 1983).

1.7.   Beyond trichromacy in infants: How is infant colour perception organised?

It has been established that infants possess trichromatic vision which

operates in a similar way to that of adults, although with certain limitations such as

the need for larger colorimetric differences and a reduced ability to discriminate at

lower saturations. Another question, now it has been firmly established that

infants are trichromatic, is what infants actually do with this trichromatic colour

vision – in other words, how do they perceive colour? This question as to how

infants make use of their trichromacy, and how their perception is organized is the

central question of this thesis. Preliminary studies of colour perception in infants

have proved promising, with researchers able to gain an insight into both infant

colour perception and infant perception more broadly. The following section will

discuss the current literature on infant colour perception and will identify and

limitations, unresolved issues and outstanding questions.

1.7.1. Infants' perception of the colour of objects and surfaces

There is ongoing debate about when infants understand colour as a constant property of an object which can be used for object identification (Wilcox, Hirshkowitz, Hawkins, & Boas, 2014). Infants 6-months-old look preferentially at items which are correctly coloured (e.g. red strawberries rather than blue strawberries) whilst infants 5-months-old do not, demonstrating an understanding of what the 'right' colour of certain objects should be may emerge between 5- and 6- months (Kimura et al., 2010). However, it is not until around 11-months-old that infants begin to use colour information to spontaneously individuate objects (Wilcox, Woods, Chapa, & McCurry, 2007). Younger infants (7.5-months) can be primed to use colour to individuate objects if there is a functional value to the colour information (e.g. the red jug does something which the otherwise identical green jug does not (Wilcox & Chapa, 2004)).

The spontaneous use of colour as a diagnostic feature of an object appears to come online quite late. One reason for this may be related to infants' development of perceptual constancies such as colour constancy. If a feature of an object is not perceived as relaying helpful information to infants due to being inconsistent, or not conveying information about the role of the object, then infants will not attend to that feature spontaneously (Woods & Wilcox, 2006).

Not a great deal is known about the development of colour constancy in humans. Dannemiller & Hanko (1987) tested colour constancy in 4-month-old infants. Infants were first familiarised to a coloured stimulus under one illumination, before being shown the familiar and novel chromaticity under one of two

illuminants, one which caused a large shift in reflectance (considered by the authors a 'true' test of colour constancy) and a second which caused a smaller shift in constancy (colour 'generalisation', or a weak test of colour constancy). If infants did *not* have adult like colour-constancy then under the new illuminant both the familiar and novel colour would appear novel, since the infants would only be using the reflectance of the stimuli, and not discounting the illuminant information, as adults would. This would result in infants looking equally at both the novel and familiar stimuli at test. In this study infants were shown to operate an immature version of colour constancy, functional only under the 'weak' test of colour constancy. Contrary to this, a second study using a similar method to Dannemiller and Hanko's (1987) study, appeared to show infants aged 20-weeks-old possessing a more mature form of colour constancy (Dannemiller, 1989). In this study, rather than using physical stimuli and illuminant, reflectances were simulated on a coloured monitor under two different illuminant conditions. The author argues that the improved ability seen by 4-month-old infants in this second study is due to the two illuminant conditions being models of daylight illumination, optimising the likelihood of infants showing colour constancy as colour constancy is argued to be optimised for illuminants along the daylight axis (Worthey, 1985). A final study (Yang, Kanazawa, Yamaguchi, & Kuriki, 2013) also demonstrated that 4.5-month-old infants are colour constant again using a habituation method with stimuli rendered under different illuminations on a CRT monitor. One interesting consideration is that 2D stimuli displayed on a CRT monitor may not provoke the same colour constancy mechanisms as real physical objects illuminated by real illuminants.

Some studies have used more realistic rendering of objects to investigate

differences in the perception of surface properties in infants. Two studies which

have used this more realistic rendering of objects have investigated infants' ability

to discriminate between properties of surfaces. The first suggests that infants from

7 months old discriminate between a metallic yellow (gold) and yellow, but not

metallic green and a matt green (Yang, Kanazawa, & Yamaguchi, 2013). This age

also appears to be the point when infants can discriminate more generally

between glossy and matte objects (Yang, Kanazawa, Yamaguchi, & Motoyoshi,

2015), and so it appears that from 7 months of age is the point where infants are

potentially more attentive to the interaction between colour and surface

properties of objects. However, as is well understood, a note of caution is needed.

The study of object and surface perception and its interaction with colour in

infancy is made particularly complicated by the developmental sciences' reliance

on infant looking responses which need to be interpreted carefully. There are

many factors which can drive infant looking, such as salience, preference, and

contrast, and that stimuli can be preferred for both novelty and familiarity

(Houston-Price & Nakai, 2004).

1.7.2. Infant Colour Preference

Infant colour 'preference' is of interest for two main reasons, firstly it can

provide insights into the origins and development of adult aesthetic preference

(both in general and for colour), and secondly, it can broaden our understanding of

what influences infant looking behaviour. On the topic of aesthetics, infants do

often look for longer at visual stimuli which adults find more aesthetically pleasing

(Damon, Mottier, Méary, & Pascalis, 2017; Quinn, Kelly, Lee, Pascalis, & Slater, 2008). Although there are commonalities in the patterns of behaviours of adults and infants, it is intuitive that there is likely a distinction to be made between an affective aesthetic preference and infant looking times. There is a wide range of both bottom-up and top-down factors additional to aesthetic preference which may work together to influence looking (e.g. salience, novelty, and complexity). Nevertheless, commonalities between infant and adult colour preference may indicate a biological origin of adult aesthetics, or the presence of 'perceptual primitives' which guide perception early on (Ramachandran & Hirstein, 1999).

Many of the studies which make up the foundation of our understanding of infant colour vision and colour perception are centred on the discovery that infant looking behaviour to colour is a reliable measure. Bornstein (1975) presented pairs of monochromatic lights to 4-month-old infants and found infants looked for longer at the colours which adults had rated as more pleasant, and suggested a sensory mechanism behind this recorded response to colour. However, monochromatic lights are not representative of the stimuli found in the natural world, leading some to question the validity of the results. Subsequent studies of infant colour preference have used either physical stimuli or rendered colours which are more representative of chromaticities commonly found in the world. Several studies have reported that infant looking behaviour does not always align with adult preference (Peltola, Leppanen, Palokangas, & Hietanen, 2007), suggesting that adult aesthetic preference to colour is not the result of low-level sensory mechanisms, but instead is formed as a result of experience (see Schloss, Poggesi, & Palmer, 2011 for an example of adaptive preferences in adulthood).

However, few studies have actually directly compared infant looking and adult preference with the same set of stimuli, making it difficult to rule out completely an early biological mechanism in either infant or adult preference. Similarly, as our understanding of chromatic thresholds in infancy has grown, it has become more apparent that the same colour shown to adults may not be easily discriminable to infants, particularly at lower saturations where infant colour vision is most limited (Zemach & Teller, 2007). As a result, despite several studies comparing infant looking to adult preference, it is unclear how similar or dissimilar the two measures are, leaving questions about the development and origins of aesthetic preference unanswered.

1.7.3.   Infant Colour Categorisation

There is converging evidence that infants categorise colour (see Franklin, 2015 for a review). Many studies of infant colour categorisation have used a novelty preference method where infants are first familiarised with one colour, before seeing that colour paired with a novel colour at test. Equivalent looking to both novel and familiar at test shows that the colours are not distinguished in infants' recognition memory. This method has reliably shown that infants' categorise blue, green, purple: that is, for example, that their recognition memory treats different blues as if they are equivalent despite chromatic differences being large enough for infants to discriminate (Bornstein et al., 1976; Catherwood, Crassini, & Freiberg, 1987; Clifford, Franklin, Davies, & Holmes, 2009; Franklin & Davies, 2004)

Another task used to investigate categorical colour effects in infancy is a target detection task where a coloured target is shown on a coloured background (Franklin, Piling, & Davies, 2005). Studies using this task have revealed that in 4- to 6-month-old infants, categorical processing of colour is lateralised to the right hemisphere (Franklin et al., 2008). For example, infants are faster at locating a chromatic target on a chromatic background when the colour pairs are from different categories than when they are from the same category, but only when presented in the left visual field (right hemisphere). This lateralisation switches to the left with the acquisition of colour terms in toddlers, the same lateralisation which is found in adult categorical perception of colour (Gilbert, Regier, Kay, & Ivry, 2006).

Electrophysiological methods have also provided further support for infant colour categories. ERP responses on a visual oddball task in 7 month old infants show a greater response when the deviant/oddball colour is from a different category to the standard colour than when the oddball is from the same category, even when same and different-category colours are equally discriminable (Clifford, Franklin, Davies, & Holmes, 2009). This pattern of categorical responding has previously (and since) also been found in other domains, such as phoneme categorisation (Dehaene-Lambertz & Baillet, 1998), and faces (Altvater-Mackensen, Jessen, & Grossmann, 2017), confirming that this response is domain-general, and not only a response to colour. fNIRs, a measure of blood flow to the brain similar to the BOLD response found in fMRI studies, has also been used to measure categorical responses of the infant brain to colour (Yang et al., 2016). Infants aged 5 to 7 months viewed geometric patterns which either alternated between two same

colour categories or two different colour categories, and a higher hemodynamic response was measured in the visual cortex when the pattern alternated between different rather than same category colours.

Despite the wealth and diversity of evidence for infant colour categories, substantial gaps remain. The number of infant colour categories has not been identified and it is not clear how infants actually form these categories or what (if any) relationship there is between infant categorisation of colour and language. One early study suggested a biological component underpins infant colour categories (Bornstein, 1975), but empirical evidence for this has never been provided. There are commonalities across languages in the division of colour space (Kay & Regier, 2003; Regier & Kay, 2009), and there is also evidence that some infant categories may align with those of adults . The similarities between adult colour lexicons and infant colour categories have not been fully documented or quantified. Further investigation of infant colour categories could provide a deeper understanding of why unrelated languages share similar structures in their colour lexicons. As well as giving insight into adult perception, further investigation of infant colour categorisation could also inform our understanding of the development and process of categorisation in infancy more generally. The process of colour categorisation in infancy has been likened to the development of biases in infancy such as the other-race-effect, as both may show a shift from perceptually biased responding, to incorporating socio-cognitive knowledge of the environment (Timeo, Farroni, & Maass, 2016).

1.7.4. Infant Perception of Colour Illusions

Adults' ability to perceive visual illusions are the result of physiological constraints of the visual system (e.g. negative afterimages) and/or also a computation of what is 'most likely' given prior experience (Corney & Lotto, 2007; Witzel, Racey, & O'Regan, 2017). As a result, understanding infants' ability to perceive illusions allows us to understand when infants begin to form these best representations of what is likely to occur in their environment. There are several studies which have looked at infant perception of colour illusions. The neon colour spreading illusion is an illusion where the colour of a figure spreads outside its boundaries, forming a 'glowing' transparent surface around the figure (figure 1.2a). Infants older than 5 months look preferentially at a single coloured stimulus which produces this neon colour spreading effect over a multicolour control stimulus which does not produce a neon colour effect. Infants between 3 and 5 months do also preferentially look at the neon colour spreading target, but only under certain conditions, suggesting that the mechanism for the perception of this illusion is still maturing between 3 and 5 months of age, but is not entirely absent (Yang, Kanazawa, & Yamaguchi, 2009).

The Munker-White illusion is an illusion where the same physical colour can appear very different dependent on the surroundings of that colour (figure 1.2b). There is some suggestion that perception of the illusion is the result of experiential factors, either those which are thought to arise naturally with maturation (such as scene segmentation), or as a result of experience with our environment (Linnell, Bremner, Caparos, Davidoff, & de Fockert, 2018), although currently there is not

one model which can account for the shift in perception found. There appears to be

evidence that infants older than 4-months perceive the Munker-White illusion in

an equivalent way to adults (Yang, Kanazawa, & Yamaguchi, 2010), as revealed

through a preferential looking paradigm. Infants were shown a pair of stimuli

where the arrangement of colours results in either a perceived large increase in

saturation of some components of the stimulus, or a version which does not result

in an increase in saturation. Infants looked preferentially at the version which

appears to have higher saturation. Interestingly, the actual perceived shift in

saturation appears to be quite small, and is possibly smaller than infants'

saturation discrimination thresholds, potentially casting doubt on the conclusions

of the study.
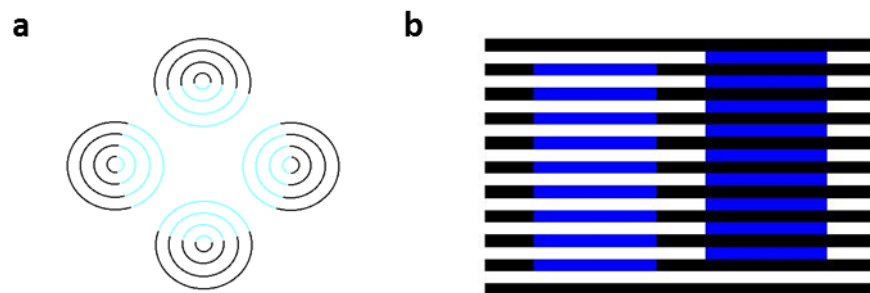
Figure 1.2. a) Neon Colour Spreading. The inner portion of the image is white, but

appears to be slightly bluer than the surroundings. b) The Munker-White

Illusion. Both shades of blue are physically identical, but our perception of

them differs dependent on their surrounds.

The study of visual illusions in infancy is complicated. Ideally, studies would be designed such that there would be clear patterns of behaviour predicted which can only be the result of an in/ability to perceive the illusions in infancy (as used in Pereverzeva & Teller, 2009). Past studies instead have often used preferential looking paradigms, predicting that preferential looking in either direction (either towards an illusory target, or at its non-illusory control) is evidence of an infant's ability to perceive the illusions. Preferential looking clearly demonstrates an infant's ability to discriminate between two stimuli. However, without an effective control however it is difficult to isolate if this preferential looking is actually the result of the illusion or just an ability to detect that there are some differences between two stimuli.

1.7.5. Infant Colour Perception: Summary

The preceding sections have identified that much has already been learnt about infant colour perception: for example, the age at which infants use colour information in object processing, that they can categorise colour, and potentially that they experience chromatic visual illusions. However, limitations in the study of infant colour perception have come to light with our increasingly fine-tuned understanding of the development of infant colour vision. For example, infants' ability to discriminate colour is poorer at lower saturations than adults, and infant chromatic discrimination thresholds are also poorer than adults, both of which need to be taken into account when designing experiments on infant colour perception. Other limitations are also found in the methodological controls and

paradigms often used in infant colour perception studies. In order to gain an accurate insight into the shape and nature of infant colour perception rigorous methods such as psychophysical methods and paradigms with clear predictable outcomes and interpretations should be applied where possible.

Although we have already learnt much about infant colour perception, there remains little understanding of the mechanisms which underlie many of the phenomena of colour perception which are found in infancy. One example is that of colour categorisation. Converging evidence presents a strong case for infant colour categorisation as demonstrated across a range of studies, labs, and methods, but there is very little known about *how* infants colour categories are formed in the absence of language. It would be advantageous to our understanding of infant colour perception to gain a better insight into the connecting processes between sensory mechanisms and behavioural outputs. It is also important to note that this need to better understand the connection between sensory input and perception is not unique to the domain of colour perception.

There is also substantial uncharted territory in the field of infant colour perception, with exciting questions not yet investigated. For example, there are many phenomena of adult colour perception which have not yet been probed in infancy. As discussed previously, adults' discrimination of saturation is unequal across hues, with larger discrimination thresholds in the blue-yellow direction. Establishing whether infants' chromatic sensitivity is also aligned to the statistical distribution of chromaticities in natural scenes would provide a critical insight into when and if infants are sensitive to natural scene statistics, and add a depth of

understanding to the growing understanding of infant statistical inferences more generally.

1.8.   Infant perception of stimuli other than colour

The study of infant colour perception is of course situated in a much larger endeavour to understand infant perception of multiple types of stimuli. The broader field of infant perception is therefore briefly summarised here. Our understanding of infant perception has moved on from the now (in)famous idea of an infants' world being *"one great blooming, buzzing confusion"* (James, 1890). Early debates in developmental science were characterised by theoretical debate between the idea of knowledge being either "built in" to infants (Nativism), or developing only as a result of learning and experience (Constructivism) (Barrouillet, 2015). More recently, there is has been acknowledgement that there is no evidence for an either/or account of the development perception and an understanding that it is unreasonable for infant behaviour to be a simple split between being purely innate or learnt. Rather it is acknowledged that infants' perceptual and cognitive skills are undoubtedly part of a more complex system, with multiple levels of developmental progress (e.g. biological maturation, and development of domain specific cognition) (Spencer, Thoman, & McClelland, 2009). More recent models of constructivism explain cognitive growth as an increase of complexity of internalised schemas (such as categorical or quantitative thought). These schemas co-develop alongside improvements in infants' processing efficiency and working memory (Arsalidou & Pascual-Leone, 2016),

although there is disagreement on the mechanisms which allow infants to progress

across through development. For example, some consider consciousness as the

causal influence in developmental progression (Spanoudis, Demetriou, Kazi,

Giorgala, & Zenonos, 2015), whilst others implicate the development of attention

as a necessary condition for progress (Halford, Cowan, & & Andrews, 2007;

Pascual-Leone & & Baillargeon, 1994).

Despite a range of theoretical proposals we still know relatively little about the

integration of the mechanisms which give rise to cognition and perception.

Consider for example, object perception. At birth, infants are functionally able to

see the component parts of a visual scene, they can see edges and motion, but do

not yet have an adult-like understanding of objects. Over the first few months

postnatally, infants' cognitive abilities develop to allow them to perceive objects as

physical entities in a real world (Johnson, 2010). The development of the cognitive

processes needed for this to happen has been well documented. For example,

whilst 2 month old infants are able to perceive an image of a rod and box to be a

single rod occluded by a box, neonates perceive the same scene as having three

component parts (the box, and two rods)(Johnson, Davidow, Hall-Haro, & Frank,

2008; Slater, Johnson, Brown, & Badenoch, 1996; Alan Slater et al., 1990). The

ability to perceive objects as complete is dependent on the development of

cognitive skills such as spatial and spatio-temporal feature binding (Johnson,

2010). Despite tracking of the individual components necessary for holistic

processing of the environment, research on the integration of these individual

skills and the implementation of these abilities in learning is needed to understand

how the perceptual system becomes optimised in adult perception (Yermolayeva &

Rakison, 2014).

1.8.1. The roles of experience and sensation in infant perception

Perceptual development is the result of both a maturation of low-level sensory processes, and also experience related factors (Timeo et al., 2016). One illustration of this is found in infants' phoneme discrimination. Infants aged 6-8 months, but not those aged 10-12 months, are able to discriminate between consonant sounds from two languages which were unfamiliar to them, whilst all infants (aged 6 months above) in this study could discriminate between consonant sounds from their own language (Werker, Gilbert, Humphrey, & Tees, 2016). This is thought to be the result of exposure to their native language, and a lack of exposure to alternative languages. This process is commonly referred to as 'perceptual narrowing' where experience (either through repeated exposure to certain stimuli or the absence of examples of a stimulus) shapes an infants' perceptual abilities (Scott, Pascalis, & Nelson, 2007). These biases can lead to a refinement of the infant sensory systems; the maintenance of neuronal connections is dependent on their usage prior to synaptic pruning. Connections which are commonly used remain, whilst those which have been inactive are lost (Luna & Sweeney, 2004). As a result, development can change the way in which information is represented.

Studies of face perception in infancy have also well documented the relationship between early sensory biases and experiential factors in infant cognition. Neonates appear to have an inbuilt range of biases which guide attention to face-like stimuli.

Rather than being a bias to *faces,* neonates' preferential looking at face-like stimuli is a bias towards stimuli with a certain spatial frequency, with areas of high contrast and a top heavy display (Farroni et al., 2005; Johnson, Dziurawiec, Ellis, & Morton, 1991) The perceptual or cognitive tools which infants possess often serve an evolutionary adaptive purpose (Moll & Tomasello, 2010; Tomasello & Moll, 2010), and there is a clear evolutionary advantage in a bias to look towards face-like stimuli. Infants' sensory bias to stimuli is dynamic and adaptive, and changes over time as their cognitive skills also develop. When eye-tracked watching a video which contained faces, 3-month-old infants' patterns of looking were best predicted by regions of low-level visual salience, such as regions of high saturation or colour, rather than faces. Between 3- and 9-months-old there is a gradual shift in looking behaviour from these 'sensory driven' areas of interest towards the faces in the video (Frank, Vul, & Johnson, 2009).

This face bias also becomes more specific, with infants aged from between 6- to 9-months-old looking preferentially faces of their own ethnic group rather than faces of a different ethnic group (Kelly et al., 2007, refered to as 'the other race effect'). This 'other race effect' is accompanied by an increased recognition of faces from own rather than other races. As in phoneme discrimination, many central theories about the emergence of this bias both point towards perceptual narrowing. Exposure to faces is often limited to those of the same ethnic group, as well as related to socio-cognitive factors such as an increased likelihood of those of the same ethnic group to be individuated (e.g. the label 'James', rather than 'the man', to distinguish our friend James from a stranger in the street) (Scott & Monesson, 2009; Tanaka & Pierce, 2009).

Parallels have been drawn between face and colour perception (Timeo et al., 2016). For example, both colour categorisation and face perception are sensitive to cultural variation. Evidence has shown, for example, that infants make a categorical distinction between green and blue, whilst there are many languages which do not, demonstrating that our perception of colour, like face and phoneme perception, can change according to the social demands of a child's environment. This also demonstrates a central facet of infant cognition; the need for cognitive abilities to be both stable and plastic over time, although what provides this stability over time is not well understood, nor is the way that across development this stability continues to be represented or manifested.

Both colour perception and perception in other domains show elements of universal patterns in behaviour. Colour perception is initially driven by low level sensory mechanisms as evidenced for example by infants' preference for stimuli with high contrast, which in turn is part of the reason for infants' early preference for face-like stimuli. These patterns of behaviour are found in infants across cultures, and there is evidence for common neural correlates across tasks requiring domain general cognitive skills (Quinn, Westerlund, & Nelson, 2006). These commonalities in perception suggests an underlying structure upon which very early perception is based, although little is known about either the time course or development prior to linguistic, cultural, or experiential influences on perception.

1.8.2. Statistical perception in infancy

A sensitivity to the structure of the visual environment makes the processing of a complex world as efficient as possible, and provides a frame around which infants can learn about their environment (McClelland et al., 2010). Research has shown that infants can extract statistical regularities from auditory, visual, and audio-visual streams (Marcus, Vijayan, Bandi Rao, & Vishton, 1999; Yurovsky, Yu, & Smith, 2012). Infants are able to extract information about these statistical streams, such as rules about which stimuli follow each other, and also use statistical patterns to shape their cognition. For example, infants 6.5-months - old familiarised to a continuum of faces with a bimodal distribution will form two face categories for this continuum, whilst those familiarised to a unimodal distribution will form a single category (Altvater-Mackensen et al., 2017 and see Maye, Werker, & Gerken, 2002, for a similar example from phoneme perception).

Faces and phonemes are just two examples from the huge number of statistical regularities which we are exposed to daily. Natural scenes contain a large amount of statistical information such as spatial frequency, and variability in chromaticity. Currently infants' sensitivity to natural scene statistics is not understood. Most studies suggest that sensitivity to natural scene statistics starts around 9 years old (Ellemberg, Hansen, & Johnson, 2012), and there is only one study with infants (Balas & Woods, 2014). That study suggested that 9 month olds look for longer at stimuli which resemble natural rather than synthetic textures, but only when the contrast of the image is inverted. The authors suggest that 9-month-old infants are therefore sensitive to natural scenes and are sensitive to deviations from typical appearance. However, it is not clear that the looking behaviours in this study are

not the result of other perceptual biases in the visual system rather than a sensitivity to natural statistics.

Understanding if infants are sensitive to natural scene statistics will tell us more about the processing of statistical regularities in infants, and will give us an understanding of the domain generality of statistical awareness. As outlined earlier there are biases present in adult colour perception which align with natural scene statistics (poorer discrimination along the blue-yellow axis along which there is the greatest variation in natural scenes). Establishing if infants also show such a bias would further our understanding of infants' statistical processing more generally.

1.8.3. Progress in Developmental Science

Across developmental science, there is a need for insight into the perceptual processes which lie between sensation and behaviour in infancy. Much research into infant perception and cognition has focussed on domains which are inherently social, such as face perception or language acquisition. Studying these domains are, of course, critical to understanding the development of infants, not least because all cognitive development does invariably take place within a social context, regardless of how 'social' it may or may not be (Bjorklund & Causey, 2017). Investigation of areas which are not inherently social in nature, such as numerical cognition, probability estimation, and colour perception in infancy can help researchers to fully characterise infant development, by separating out which processes are domain general and which are domain specific.

Many of the findings of in studies of colour perception have implications for infant perception more generally, and colour provides a carefully controlled stimulus to examine aspects of infant perception and to verify their domain generality. For example, much of infant perception is based on the chunking and integration of information from continuous variables (colour, faces, orientation, texture, etc.). Creating a carefully controlled stimulus set is markedly easier with colour than it is in other domains. This is because our perception of colour can be modelled accurately by the underlying sensory mechanisms of the colour vision system. There are fewer degrees of freedom in colour than there are in other variables, such as faces for example. This allows researchers to more easily connect the underlying sensory mechanisms influence on behaviour in infants.

1.9. Thesis Overview and Research Questions

The current thesis investigates 4 aspects of colour perception in infancy; colour categorisation, colour preference, perception of colour illusions, and the sensitivity of infants to colour in natural scenes. These topics provide an insight into how infant colour perception operates once infants are trichromatic. We know much about the anatomical development of the infant visual system, but in order to fully understand infant perception both in colour and other domains, it is necessary to attempt to understand how an infant might use structures such as trichromacy to shape their perception of the world.

How do infants categorise the continuum of hue, and what are the underlying mechanisms that enable them to do this in the absence of language? Is there an

early basis for aesthetic preference for colour: do infants look longer at colours that adults like? Are the perceptual processes which underlie the perception of chromatic illusions present and integrated in infancy? Do infants show the same statistical biases in colour discrimination as adults do? Or is this bias learnt across the life span? These questions all get to the heart of a central debate in developmental science about how low-level sensory processes interact with the role of experience or our environment to shape our perception of our world. They also cast light onto the origins of our perception as adults. As well as being concerned with colour and infant perception, these questions also address broader fundamental debate in the cognitive sciences such as the relationship between language and thought (Regier, & Kay, 2009), how early sensory response to allows for adaptations to our environment (Bjorklund, 2015), and the origins of aesthetic preference (Ramachandran, & Hirstein, 1999).

The thesis addresses each of these questions by presenting 4 papers which each investigate an aspect of infant colour perception. The following sections provide summaries of each of these papers.

1.9.1. Paper 1 – Biological Origins of Colour Categorisation

Paper 1 (Skelton, Catchpole, Abbott, & Franklin, 2017) investigates the origin and mechanisms of colour categorisation in a large scale infant study. As outlined earlier, there has been much debate on whether colour categorisation is innate or culturally relative. Relativists argue that colour categories are defined by language making arbitrary divisions of the colour spectrum, resulting in variation

in colour lexicons across languages (Roberson, Davies, & Davidoff, 2000;

Roberson, Davidoff, Davies, & Shapiro, 2004). Contrary to this, Universalists point

to commonalities in the organisation of colour lexicons, such as the stability of

colours commonly chosen as category centroids across languages, to suggest that

there are universal constraints on how language divides up the colour spectrum

(Kay & Regier, 2003; Lindsey & Brown, 2006; Regier, Kay, & Cook, 2005). One

possibility related to the Universalist position is that colour categories are

hardwired and determined by the biological mechanisms that underpin colour

vision. Support for a biological account of colour categorisation is found from

studies which provide evidence for infant colour categories despite infants being

pre-linguistic (e.g. Bornstein et al., 1976; Catherwood, Crassini, & Freiberg, 1990;

Franklin & Davies, 2004; Yang et al., 2016). However, as outlined earlier, there are

many unanswered questions about infant colour categories: in particular, the

number and location of these categories across the colour spectrum; how these

categories are formed; and how these infant colour categories relate to adult

colour lexicons.

Paper 1 aimed to address these questions by mapping the colour categories of

infants (4- to 6- months-old) using the World Colour Survey (WCS) stimulus grid

which has been used to map the world's colour lexicons. This was done using a

method based on infant recognition memory called novelty preference. The

principle of novelty preference is that following habituation to one stimulus,

infants will look preferentially at a stimulus they judge to be different to the

familiar stimulus they were habituated to (Mareschal & Quinn, 2001). A failure to

look preferentially at a novel stimulus during the test phase following habituation

indicates that familiar and novel stimuli are being treated equivalently by the infant. If these stimuli are nevertheless discriminable to the infant, then a lack of novelty preference fits the classic definition of categorisation that 'discriminable stimuli are treated equivalently' (Quinn, 2003). In paper 1, infants were familiarised to a hue from the World Colour Survey before it was paired at test with the adjacent colour from the stimulus sample. This was repeated for 16 stimulus pairs, and the novelty preferences were analysed to establish which colour differences infants distinguished in their recognition memory and which colours were treated as if equivalent.

Novelty preference scores are calculated (looking time to the novel hue in comparison to the familiar hue), and pairs of stimuli where infants looked preferentially at the novel stimulus at test are considered to be the location of an infant colour category boundary. Novelty preference scores for the colour pairs tested revealed infants' recognition memory divides the colour continuum into red, yellow, blue, green, and purple categories. There were no significant novelty preferences for colour pairs within these categories, even when colour differences were large. Crucially, infants' novelty preference could not be explained how similar the colours in each pair were (perceptual similarity). Infants' significant novelty preference response at category boundaries was not the result of colour pairs in these locations being easier to discriminate than other pairs. This was revealed by regressions which showed differences in hue, chroma, or Euclidian distance calculated in perceptual colour spaces did not predict infant novelty preferences. Further evidence came from data collected from adults on the similarity of hues in a stimulus pair, which did not predict infant novelty

preference either. Using a target detection task, we ruled out the possibility that infants' non-significant novelty preferences (i.e. pairs within category) could be explained as an inability to discriminate colours in a pair. In this task, infants' likelihood of fixating a chromatic target on a chromatic background did not relate to infant novelty preference for the same pair of colours in the main study. From these additional analyses and control experiments we can conclude that the pattern of infant novelty preferences can be accounted for by categorical recognition memory rather than lack of discrimination or perceptual similarity.

The next stage in the study was to investigate the underlying mechanisms of infant colour categorisation – what guides infants division of colour into five categories? By plotting infants' novelty preferences in a colour space that represents the early encoding of colour, paper 1 found that four of the five category boundaries align relative to the adaptation point with the cardinal axes that describe the early representation of colour in retinogeniculate pathways. This alignment points to a biological basis for infant colour categorisation.

Infant colour categories were then compared to the categories found in the world's colour lexicons. Striking commonalities were found between infant colour categories and the documented similarities found across adult colour lexicons documented in the World Colour Survey. Paper 1 revealed that infant colour categories are organised around hues which are commonly found to be at the centre of colour categories across languages. Infant colour categories were compared to data on the location of category centres from the World Colour Survey. A permutation analysis found that the infant pattern of categorisation

captured these commonalities in centroids found in adult colour categories better than 95% of all possible permutations of the same number of category boundaries.

Paper 1 supports previous studies which had found that infants categorise blue, green (e.g. (Catherwood et al., 1990), purple (Franklin & Davies, 2004), red and yellow (Bornstein et al., 1976), and provides the first evidence that infants also distinguish between purple and red. It is also the first to systematically sample at regular intervals from around the complete hue circle in order to capture infant colour categories. This enables the ground-breaking finding that infant colour categories are related to early encoding of colour in the retinogeniculate pathways. The study makes a critical contribution to the ongoing debate between Universalists and Relativists on the nature of colour categories and their lexicons as paper 1 provides concrete evidence that colour categories are not arbitrary. Instead colour categories are constrained in early development by the biological mechanisms which underpin colour vision, and these fault lines form the building blocks of adult colour categorisation across languages.

1.9.2. Paper 2- Infants look longer at colours that adults like when colours are highly saturated.

Paper 2 compared adult aesthetic judgements and infant responses to colour to investigate if there is an early basis for aesthetic preference for colour. Although adult aesthetic preferences appear to idiosyncratic, there is a suggestion that aesthetic judgements are an interaction between visual sensory processes and early perception, and on judgements based on higher order cognitive mechanisms,

such as cultural experience (Schulz & Hayn-Leichsenring, 2017). If some aspects of aesthetic judgments are based in early processes in the visual system, then we may expect some parallels between infant and adult response to stimuli. For some visual stimuli, such as faces (Damon et al., 2017), this does appear to be the case as infants look for longer at stimuli which adults prefer. This raises an interesting debate on what underlies infants' response to stimuli, as well as what adult aesthetic judgements are based on.

In the domain of colour, adult aesthetic judgements have been shown to be very reliable with the same pattern of colour preferences being reported multiple times (e.g. Jastrow, 1897; Palmer & Schloss, 2010). If it is the case that aesthetic judgements are in part governed by sensory processes, then we may expect to see the roots of adult preferences in infant behaviour. However, as outlined earlier, previous studies that compare infant and adult colour preference have given conflicting reports on the similarity of adult aesthetic judgements and infant looking time to hues (Adams, 1987; Hurlbert & Ling, 2012; Taylor, Schloss, Palmer, & Franklin, 2013). These conflicting outcomes may be the result of some of these studies using de-saturated stimuli that do not account for infants' poorer discrimination of colour at lower saturations (Teller, Brooks, & Palmer, 1997).

In paper 2 infant looking times to an extensive set of hues were related to adult aesthetic judgements. The stimuli were all maximally or very highly saturated, ensuring that infants would be able to detect the stimuli. Data was taken from paper 1 on infant looking times for multiple hues. In addition, adults were shown each hue individually under the same illumination conditions which infants viewed the colour, and asked to rate on a scale how much they liked or disliked each

colour. There was a significant correlation between infant looking time and adult preference for colours; when colours were highly saturated, on average infants looked for longer at the colours which adults preferred. Both infants and adults showed a peak in response to blue hues, and a minimum for green-yellow hues. Comparison of the measures for infants and adults with how colours activate the retinogeniculate pathways showed that responses could be partially summarised in terms of how colours activate the blue-yellow neural pathway of colour vision.

These findings suggest that there is an underlying sensory component to infants' looking preferences which later manifests as an aesthetic preference in adults. This study is one of few to present the same set of colours to adults and infants, and also carefully considers the development of infant colour perception in its stimulus selection. Paper 2 has implications for our understanding of what drives infants' responses to stimuli, Infant looking to colour does not necessarily reflect their affective response to colour, as there are a variety of processes and reasons an infant may look longer at a stimulus, such as novelty or complexity. Paper 2 provides an insight into how sensory mechanisms may bias infants' response to colour.

1.9.3. Paper 3 – Further investigation of the perception of the Munker-White illusion in infancy

Paper 3 examines the perception of the Munker-White illusion in 4-8 month old infants. This illusion, where the same colour appears to shift in hue, saturation, or lightness (or any combination of the three) depending on context, is thought to

be the result of a combination of both high and low level visual processes (for example assimilation (Ripamonti & Gerbino, 2001), and scene segmentation (Anderson, 2003). Studying the Munker-White illusion in infancy provides insight into when and how perceptual processes develop and integrate, and also gives more information about the processes behind the perception of illusions in adults.

As discussed earlier, one previous study (Yang et al, 2010) suggested that infants can perceive the Munker-White illusion. However, the perceived difference in colour caused by the illusion, although detectable to adults, is subtle and possibly below threshold for saturation discrimination in infancy (e.g., see Knoblauch et al., 2001 for infant thresholds). The first study of paper 3 is an attempt to replicate the original study by Yang et al (2010). Replication in developmental science is particularly important due to a noisy participant population and common variation in effect sizes found across studies (Duncan, Engel, Claessens, & Dowsett, 2014). In the second study of Paper 3 a habituation paradigm is used to further investigate the perception of the Munker-White illusion in infancy.

In experiment 1, two stimuli were used which to adults appear to be made up of different colours, even though the component colours of both stimuli are physically identical. Due to the spatial arrangement of these colours, the yellow component of one stimulus appears more saturated than it does in the other stimulus. These stimuli are presented to infants, and looking times are recorded. The expectation is that if infants do perceive the illusions, they will look for longer at the stimulus which appears to be more saturated. However, despite identical method, sample size and analysis, we did not replicate the findings of Yang et al: infants did not

look significantly longer the stimulus which is perceived to adults as being more saturated.

Experiment 2 aimed to address some of the stimulus and design limitations of Yang et al,'s study, by using stimuli that are clearly discriminable for infants, and having appropriate control of a priori preferences. The second experiment used a habituation paradigm where infants were familiarised to the illusion before a test phase which was designed to elicit 2 different patterns of response dependant on infants' perception of the stimulus; one response if participants habituated to the physical colour of the stimulus, and another if participants habituated to the illusory colour of the stimulus. Interestingly, infants' response at test did not follow either predicted pattern of response: they looked at all stimuli equally. One potential explanation is that infants were distracted by one component of the stimulus (the striped background) rather than processing the stimulus holistically which would be needed to experience the illusion.

Paper 3 reopens the question of whether infants experience the Munker-White illusion, and also raises questions about the integration of perceptual processes in infancy. The paper provides lessons in conducting research on visual illusions in infancy. This paper also highlights two methodological issues relevant to developmental science and broader topics within perception; firstly, the importance of tight control and design of stimuli, and secondly the value of replicating research within noisy population groups.

1.9.4. Paper 4 – Colour vision is aligned with natural scene statistics at 4 months of age

The adult visual system is optimised to represent the statistics of the natural world. For example, when the spatial frequency characteristics of images are similar to those found in natural scenes, adults show improved performance on recognition and discrimination tasks (e.g. Párraga, Troscianko, & Tolhurst, 2000; Tolhurst & Tadmor, 2000). It is currently unknown *when* in development our visual system begins to show this alignment to the statistics of natural scenes. Paper 4 investigates whether a bias in colour sensitivity that has been found in adults and which has been related to the distribution of chromaticities in natural scenes is also present in infants.

Adult sensitivity to saturation is not equal across all hues (Bosten, Beer, & MacLeod, 2015). One method of quantifying these inequalities is to measure discrimination thresholds along the cardinal directions and its intermediaries, and fit a discrimination ellipse through the resulting threshold points. Elongation of this ellipse in a particular direction reveals poorer sensitivity along that axis. Discrimination ellipses in adults show significant elongation along the blue-yellow direction (the negative diagonal) of the MacLeod Boynton chromaticity diagram across a range of tasks. The blue-yellow axis along which adult sensitivity is poorest is close to the 'daylight axis', the direction along which the chromaticity of daylight illumination varies, between blue skylight and yellow sunlight (Pearce et al., 2014). This has led to the suggestion that adult sensitivity may be poorest along this axis as a result of chromatic tuning to the chromaticities most common in

natural scenes in order to make visual processing as efficient as possible (Bosten et al., 2015; Foster, Nascimento, & Amano, 2004).

Paper 4 measures infant and adult discrimination ellipses, and estimated thresholds around the hue circle. We recorded infants and adults eye-movements whilst being shown a coloured target on a grey background to measure their ability to see the colour. Thresholds were measured for 8 colours and for each colour there were 8 levels of saturation. The method of constant stimuli was used which provided full psychometric functions for infants and adults for each colour. These psychometric functions were then used to estimate thresholds for each colour and these were then used to fit a discrimination ellipse.

Infants and adults both showed reduced sensitivity along the blue-yellow axis, being poorer at detecting blue and yellow targets. There was therefore evidence that infants displayed the characteristic blue-yellow bias in the discrimination ellipse found in prior adult studies. These findings suggest that either the mechanisms underlying the tuning of colour perception to natural scenes are innate, or the calibration to natural scene statistics happens very early in development, between 2- 4 months (between the points when trichromacy first develops and the youngest participants in paper 4).

Paper 4 also sheds new light on the measurement of psychometric functions in both infants and adults. The likelihood of target detection in the task is the combination of many factors including visual sensitivity, attention, motivation, and gaze control. Each of these factors bears an influence on performance, and can be described via its own psychometric function, with the psychometric functions measured in paper 4 being the outcome of the combination of these different

factors. The analysis revealed that selecting threshold criteria (alpha) at different points along the psychometric function resulted in variation in the amount of bias in the discrimination ellipse, implying that the weight of each of these factors, and its contribution to performance varies across the psychometric function. At points where performance is only just above chance (at lower alpha levels) participants psychometric functions appears to be influenced most by visual sensitivity, i.e. the weight of the psychometric function underlying visual sensitivity is greater than those governing other processes. A similar variability in thresholds collected from infant psychometric functions across alpha criterion has been reported when using an adaptive staircase procedure with infants (Jones, Kalwarowsky, Braddick, Atkinson, & Nardini, 2015), here we report similar effects when using the method of constant stimuli.

Paper 4 provides the first firm evidence that the infant visual system is aligned with natural scene statistics, and provides a developmental window during which alignment could take place. Paper 4 also has implications for our understanding of statistical learning in infancy (see Saffran & Kirkham, 2018 for a review), as it demonstrates that sensitivity to statistics in an infants' environment is found for colour. Previous studies have found other types of statistical learning in infancy, such as statistical learning of sequences (e.g. Kirkham, Richardson, Wu, & Johnson, 2012; Saffran, Johnson, Aslin, & Newport, 1999), although generally statistical sensitivity has been demonstrated at an older age than is found in Paper 4. There are also implications for the development of tasks that are appropriate for threshold measurement in infancy (Jones, Kalwarowsky, Atkinson, Braddick, & Nardini, 2014; Jones, Braddick, & Atkinson, 2015). Paper 4 demonstrates that

careful consideration should be given when defining threshold criterion for analysis. It also shows that full examination of psychometric functions can reveal insights into the different processes guiding performance, and the different processes underpinning cognition across performance.

1.10.   Overall Contribution

The papers in this thesis demonstrate that the roots of mature colour perception are found in infancy and in the physiology of early colour vision. Previous discussions of the development of colour perception have underweighted the input of these early biological mechanisms and their shaping of our perception, instead weighting the role of experience far more heavily than may be necessary. Whilst the role of experience clearly does have a large influence on perceptual development, it is important to appropriately account for the relative weightings of biological mechanisms and experiential factors to enable a more detailed overview of development. This highlights one of the main benefits of examining perceptual processes in infancy. Behaviour is revealed not to be entirely idiosyncratic but instead to share a common element across individuals which is revealed in measuring infant response to stimuli. With an increasing understanding of appropriate measurement of perceptual phenomena in infancy, we are also able to gain a greater insight into the workings of adult perception.

Several of the papers cause us to challenge current theories and debates in cognitive science. For example, our demonstration of how the retinogeniculate pathways provide the fault lines of infant colour categorisation propose a

challenge to Relativist theories of categorical perception. Similarly, the evidence of an underlying influence of sensory mechanisms in colour preference in infant and adult response to colour demonstrates that it is unlikely to be interaction with objects alone (ecological valence theory) which influences our aesthetic preference of colour. Both these findings indicate a common starting point to our perception of colour. We can also begin to see how infant perception of colour has implications and consequences for adult perception of colour. It appears that the underlying mechanisms of our colour vision provide guidelines upon which our interaction with objects and the environment can build upon.

The extent to which these findings are specific to colour or are the result of domain general mechanisms has important implications for our understanding of the development of broader cognitive skills and developmental theory. Underlying sensory biases and structures have been suggested by some (e.g. Bjorklund, 2015, Barrouillet, 2015) to increase the chance of a positive adaptive response to their environment, and as a result, represent the ability for infants to extract meaningful information from their surroundings. We are able to see from the papers in this thesis that infants are drawing on information in the world around them (e.g. paper 4), and that their sensory apparatus to helps inform their perception and behaviour of the world.

1.11. Future Research

The field of infant colour perception is a diverse and exciting one with many outstanding questions which can contribute to ongoing debates in both perception

and developmental science. There remains much to be learnt about how infants'

colour perception is structured, both through development of some of the central

questions presented in the papers of this thesis, and in areas beyond the scope of

the current thesis where we know very little, such as the development of colour

constancy or the cortical processing of colour in infants. Here follows a brief

outline of some outstanding questions in infant colour perception.

Firstly, how is the journey from biologically constrained colour categories to a

culturally informed colour lexicon made? There is currently a gap in our

knowledge of how infants learn to abstract colour from properties and successfully

map colour words to their internal representation of colour categories. There may

also be broader implications for understanding the development of the 'skill' of

categorization more generally, as similarities have been drawn between colour

word learning in childhood and factors which have been shown to moderate

category learning, such as perceptual salience, input frequency, and category size

(Yurovsky, Wagner, Barner, & Frank, 2015). There has been preliminary work to

find the beginnings of an ability to attribute colour words to objects via a referent

selection task (Forbes & Plunkett, 2017), but how perceptual categories relate to

lexical categories across development is not understood. Mapping colour

categories and colour word acquisition across the developmental life span can

enable researchers capture this transition to help identify how our cultural

experience builds upon the fault lines provided by our visual system.

Other means of approaching this question can also be found in brain based

measures such as fNIRs. fNIRs has previously been used to demonstrate

categorical responding in the infant cortex (Yang, Kanazawa, Yamaguchi, & Kuriki,

2016), meaning it may be possible to map infant and children's categorical response to colour by measuring cortical response to colour categories across early developmental lifespan. This would allow for comparison of the development of lexical categories found with studies of young children to the underlying representation of colour in the cortex, giving an exciting insight into how the interaction of low level mechanisms and cultural influence shapes our perception of colour.

The second question to be asked in future research is how and when infants acquire colour constancy. Understanding the development of colour constancy is possibly critical to our understanding of the progression from biologically constrained colour categories to mature culturally varying colour lexicons, as there would appear to be an advantage in having colour constancy when children attempt to understand what the, for example, green part of an object is. Currently very little is known or understood about the development of colour constancy, although there have been recent advancements in our understanding of perceptual constancy more broadly (e.g. Yang, Kanazawa, Yamaguchi, & Motoyoshi, 2015; Fleming, 2015) It has been suggested that 7-month-old infants perceive constant surface properties, whilst 5- and 6-month-olds do not, putting forward the idea of a 'pre-constancy' phase of infant development (Yang, Kanazawa, Yamaguchi, & Motoyoshi, 2015). However, disentangling whether infants' response is the result of low-level stimulus properties rather than a holistic integration of cues present in the stimuli can be difficult, and it's in this area where research should be focused (see Witzel, O'Regan, & Hansmann-Roth, 2017 for discussion of the surface properties of Yang et al's (2015) stimuli).

A third question arises from our finding that infants are sensitive to natural scene statistics from as young as four-months-old. If infants are raised in an environment with a different pattern of variance in chromaticity, do they show alignment with their environment, or is the blue-yellow bias genetically determined? Currently, the majority of current hyperspectral image sets depict natural scenes which do show a blue-yellow bias, but it is likely that there are environments where the chromatic distribution of scenes may not show the same amount or direction of variation (e.g., a lush jungle). Similarly, the variation in chromatic scenes which we are exposed to may be markedly different within the same geographic region across the year (e.g. the Arctic Circle; Laeng, Brennen, Alden, Paulsen, Banerjee, & Lipton, 2007), which could lead to different patterns in early tuning if this effect is the result of experience rather than a biological unfolding.

One much needed future study would capture and quantify the variation of a range of natural scene statistics across cultures and environments, and then test individuals across the life span who have lived experience of a particular environment. This will help disentangle how the mature visual system is optimised for its environment, and the way in which experience and the worlds' statistical regularities interact and informs our perceptual experience. These cross-cultural approaches could use a task similar to that outlined in paper 4 in order to compare thresholds to variations in an individuals' environment, and also across the life span of different populations. Developing our knowledge of our sensitivity to natural scene statistics can contribute to understanding the mechanisms of perceptual learning across the life span, and how probabilities are represented by

the different stages of vision and perception (Pouget, Beck, Ma, & Latham, 2013).

Testing the domain generality of sensitivity to natural scene statistics beyond the

case of colour will identify how our perceptual system is (or is not) optimised to

represent the statistical regularities of our environments. A greater understanding

of these processes will also help inform developmental models of perception and

cognition in infancy, early childhood, and adults (Yermolayeva, & Rakison, 2014).

A final area for development in future is how colour information becomes

integrated with other sensory modalities. Questions about how and when cross-

modal correspondences are formed in childhood can help researchers gain a

qualitative insight into perception across the lifespan. Cross modal associations

adult colour perception are found across a number of domains, but there are

outstanding questions on their origin as they remain relatively undocumented in

infancy and early childhood. Many studies of cross-modal integration indicate that

some cross-modal experiences common to adult perception are already

successfully integrated in early infancy (e.g. colour and object, Kimura et al, 2010;

vision and auditory. Kuhl & Meltzoff, 1982; Burnham & Dodd, 2004; object and

texture, Sann & Steri, 2007), with some correspondences being 'lost' with age

(Ludwig & Simner, 2013). In addition, there are areas where children do not

integrate information from across/within domains until they are over 8 years old

(Nardini, Bedford, & Mareschal, 2010; Gori, Del Viva, Sandini, & Burr, 2008).

Understanding the *how* and *when* the brain becomes aware of such co-occurrences

of its environment over development will provide a qualitative insight into

perceptual experience of infants and children, as well as having informing models

of perception across the life span. There also remain questions about what the

advantage, both to infants and adults, the integration or lack of integration between modalities gives us in our perception.

1.12. Conclusion

The papers in this thesis present key findings on four areas of infant colour perception; the structure of infant colour categories, the origins of infant colour preference, the perception a colour illusion in early infancy, and sensitivity of infants to chromatic natural scene statistics. Two main themes emerge across these papers, firstly, infant response to colour appears guided by the low-level sensory mechanisms of colour vision, and secondly, that this structure provides the roots from which mature colour perception can then develop. For example, infants' response to colour is shaped by the underlying sensory mechanisms of the retinogeniculate pathways, and echoes of this influence of behaviour are found in adult colour lexicons and adult aesthetic judgements of colour.

There are outstanding questions particularly in exactly how experience influences our perception of the chromatic world, and how this may relate to the development of more domain general mechanisms across the life span. Advancements in methodologies of testing infants, and developments in our understanding of infant vision mean that developmental scientists are well placed to investigate outstanding questions on how infants see and think about colour.

Chapter 2 - Paper 1: Biological origins of colour categorization

2.1. Abstract

The biological basis of the commonality in colour lexicons across languages has been hotly debated for decades. Prior evidence that infants categorize colour could provide support for the hypothesis that colour categorization systems are not purely constructed by communication and culture. Here, we investigate the relationship between infants' categorization of colour and the commonality across colour lexicons, and investigate the potential biological origin of infant colour categories. We systematically mapped infants' categorical recognition memory for hue onto a stimulus array used previously to document the colour lexicons of 110 non-industrialized languages. Following familiarization to a given hue, infants' response to a novel hue indicated that their recognition memory parses the hue continuum into red, yellow, green, blue and purple categories. Infants' categorical distinctions aligned with common distinctions in colour lexicons, and are organized around hues that are commonly central to lexical categories across languages. The boundaries between infants' categorical distinctions also aligned, relative to the adaptation point, with the cardinal axes that describe the early stages of colour representation in retinogeniculate pathways, indicating that infant

colour categorization may be partly organized by biological mechanisms of colour vision. The findings suggest that colour categorization in language and thought is partially biologically constrained, and have implications for broader debate on how biology, culture and communication interact in human cognition.

2.2. Significance Statement

Humans parse the continuum of colour into discrete categories (e.g., 'red' and 'blue'), and the origin of these categories has been debated for many decades. Here we provide evidence that infants have colour categories for red, yellow, green, blue and purple. We show that infants' categorical distinctions align strikingly with those that are commonly made in the world's different colour lexicons. We also find that infants' categorical distinctions relate to the activities of the two neural sub-systems responsible for the early stages of colour representation. These findings suggest that colour categorization is partly organized and constrained by the biological mechanisms of colour vision, and is not arbitrarily constructed by language.

2.3. Introduction

The extent to which cognition is biologically 'hardwired' has been hotly

debated (Carey, 2009; Cohen, Chaput, & Cashon, 2002; Hespos & Spelke, 2004;

Wynn, 1992). Colour cognition has provided a fertile testing ground for such

debate. One key question has been the origin of colour terms and their categories.

Although the spectrum of colour is continuous, humans typically refer to colours

with a number of discrete terms (e.g., red, green, blue). Some have argued that how

terms categorize the continuum of colour and how colour lexicons evolve is

biologically constrained (Berlin & Kay, 1969; Kay, 2005), others have argued that

colour terms and their categories are culturally and linguistically constructed

(Roberson et al., 2000). Cognitive scientists from a broad range of disciplines (e.g.,

linguistics, neuroscience, vision science, anthropology, developmental science)

have been working for decades to understand how colour terms and their

categories form. These efforts have established that although the colour lexicons of

the world's languages vary in the number of colour terms and in how they parse

the continuum of colour, there is also striking commonality across languages and

evidence for 'universal' constraints (Kay & Regier, 2003; Lindsey & Brown, 2006,

2009, Regier et al., 2005, 2007). For example, in the World Colour Survey (WCS),

speakers of 110 non-industrialized languages named 320 colours (Kay et al.,

2009), and analyses have shown that the centers of the categories denoted by

these languages' colour terms cluster around particular hues (Kay & Regier, 2003).

These particular hue regions also appear to be central to the colour categories of

industrialized languages (e.g., English), and are commonly the location of the 'focal'

best examples of colour terms (Regier et al., 2005). The organizing principles for

this common categorization structure have been sought, and computational

models have suggested a number of sources such as the chromatic structure of

natural scene statistics (Yendrikhovskij, 2001) chromatic discrimination

thresholds (Baronchelli, Gong, Puglisi, & Loreto, 2010) or 'near-optimal

partitioning' mechanisms based on basic principles of categorization (Regier et al.,

2007). There has also been a hunt for neurons which encode colour categorically in

regions of the visual cortex and early ventral stream (Bird, Berens, Horner, &

Franklin, 2014; Brouwer & Heeger, 2013; Persichetti, Thompson-Schill, Butt,

Brainard, & Aguirre, 2015).

Although we do not yet have solid evidence for the neural basis of commonalities

and 'universal' constraints in colour naming, further impetus for the idea that

colour terms and categories have a biological basis has come from studies with

infants (Bornstein et al., 1976; Catherwood, Crassini, & Freiberg, 1990; Clifford,

Franklin, Davies, & Holmes, 2009; Franklin et al., 2008; Franklin & Davies, 2004;

Franklin, Pilling, & Davies, 2005; Ozturk, Shayan, Liszkowski, & Majid, 2013; Yang

et al., 2016). Converging evidence suggests that pre-linguistic infants as young as

four months old respond categorically to colour. Many of the infant studies have

relied on the 'novelty preference' method that has been used to demonstrate that

categorization is a domain-general and fundamental aspect of infant cognition

(Mareschal & Quinn, 2001). Infants are familiarized to a given hue through

repeated presentation (until infant looking at the hue wanes) and a novel hue is

then presented during a test phase. If infants look longer at a novel than familiar

hue at test (a novelty preference) then infants are deemed to distinguish the two

hues in their recognition memory. Studies have shown that infant recognition

memory appears to distinguish hues that are differentiated by certain lexical distinctions (e.g., blue-green), and infant recognition memory treats hues within these lexical categories as if they are equivalent (e.g., no novelty preference). This 'same-category' equivalence in recognition memory has been found even when hues within a lexical category are well above infants' chromatic discrimination thresholds when measured with simple detection tasks (Franklin et al., 2008; Franklin et al., 2005), and when hue differences are maximized (Franklin & Davies, 2004). Infants' responses therefore fit the classic definition of categorization: 'responding in an equivalent manner to discriminably different stimuli' (Quinn, 2003, pg 52) . Evidence for a categorical response in infant recognition memory for hue has also been provided using neuroimaging methods, such as event related potentials (Clifford et al., 2009), and near infra-red spectroscopy (Yang et al., 2016).

Infants' apparent categorization of colour suggests that colour categorization may have a biological origin. Of course, lexical colour categories cannot be completely biologically determined since colour lexicons vary across languages both in the number of colour terms and in the location of lexical colour boundaries. Communication needs, and cultural and environmental forces are inevitably valuable in explaining the evolution of a colour lexicon within a culture (Quinn, 2003). However, it is possible that lexical colour categories are partly rooted in the underlying mechanisms of the early visual system that code for colour. This partial constraint could potentially explain the commonality in categorization structure across the world's languages, such as the clustering of categories around particular

regions of colour (Kay & Regier, 2003) or the common category 'motifs' that are seen across languages (Regier et al., 2005).

Although it is theoretically possible that colour categories have biological roots, the current evidence of a categorical response to colour in infancy is insufficient for a full endorsement of this theory. First, the majority of the evidence for a categorical response to colour in infants comes from testing a few colour categories that are defined by their lexical distinction in English (e.g., blue-green and blue-purple). The full continuum of hue has not been tested and so categorical distinctions may have been missed. This means that, although there is converging evidence that infants respond categorically to colour, the number and location of infant colour category boundaries is not currently known.

A more complete characterization of infant colour categorization is needed to clarify the relationship between infants' categorical response and lexical colour categories. One possibility is that the way in which infant categories divide up the hue continuum is highly similar to the structure of colour lexicons. An alternative possibility is that infants' categorical response is a quirk of a few limited regions of colour space, and that it has little resemblance to more comprehensive categorization systems seen in language. Infant colour categories could align with those of specific languages, for example, lexicons of industrialized languages that have a greater number of basic terms than lexicons of non-industrialized languages. However, we consider it more likely that infant colour categories would align not with any one language in particular, but rather with the categorization structure that is common across the world's languages, since it is this commonality

that potentially suggests some form of biological constraint. For example, one hypothesis is that infant colour categories are organized around the hues that Kay and Regier (Kay & Regier, 2003) have revealed to be commonly at the centers of the categories of the WCS.

A second reason why there is currently insufficient evidence for the theory that colour categorization has biological origins is that the underlying mechanisms of infant colour categorization have not been systematically investigated. Infant categories, at least at 4-months, are unlikely to have communication or cultural origins, but they are not necessarily rooted in the biological mechanisms of the visual system. It is often assumed that the presence of infant categorization is evidence of a biologically determined 'innateness', yet infants also have a remarkable ability to learn categories by tuning into the statistical regularities present in stimulus exemplars (Fiser & Aslin, 2002). Environmental origins of colour categories have been proposed (e.g. Kay et al., 2009) and it is at least theoretically possible that infants are able to tune into the statistical regularities and structure of their chromatic environment in order to extract a categorization structure (Clifford et al., 2009). Another possibility is that infants' colour categorization is based on 'near-optimal' partitioning of the colour spectrum as has been argued for lexical categorization (Regier et al., 2007), with infants also applying basic principles of categorization (Garner, 1974) to an uneven perceptual colour space.

When Berlin and Kay (Berlin & Kay, 1969) first discovered the regularity in the evolution of colour terms across colour lexicons, it was proposed that colour

categories had a biological basis. However, subsequent investigation of the retinogeniculate cone-opponent pathways of the visual system that underpin the early encoding of colour has revealed that these pathways do not encode the 'basic' white, black, red, green, blue and yellow categories (and the perceptually pure 'unique' hues of these categories) as originally proposed (Jameson & D'andrade, 1997). What are commonly known as the 'red-green' and 'blue-yellow' cardinal cone-opponent mechanisms are actually better described as 'cherry-teal' and 'chartreuse-violet' in terms of the appearance of the colours they encode. The idea that the cardinal mechanisms can explain the commonality in colour categorization across languages such as good examples (focals) and perceptually pure examples (unique hues) of colour has therefore been largely dismissed. Nevertheless, there has been some recent tentative evidence for a link between the early colour mechanisms and colour categorization from a study that concluded that the 'red-green' cone-opponent mechanism accounted for the common 'warm-cool' category distinction that arises from analysis of WCS naming data (Xiao, Kavanau, Bertin, & Kaplan, 2011). It is theoretically possible that infants are able to draw on cone-opponent mechanisms in a similar way in order to categorize colours. Evidence that infant colour categorization is related to the cardinal axes of colour vision would be strong support for the theory that colour categorization has biological origins.

The current investigation had three aims: First, to establish the hue categories that infants have; Second, to establish the relationship between infant colour categories and adult colour lexicons; Third, to identify the underlying mechanisms of infant colour categorization and whether infant categories are related to the cardinal

cone-opponent mechanisms that underlie early coding of colour. Together, the findings aim to shed light on whether colour categorization has biological origins that partially constrain the formation of colour categories within a language.

In order to address these aims, we mapped infant categories onto the hue circle using the stimulus array from the WCS. We systematically sampled colours from a row of the WCS stimulus grid. Within this row, hues span the hue circle, are at constant lightness and at varying chroma (similar to saturation or colourfulness). We sampled colours at regular hue intervals that we predicted, on the basis of infant chromatic thresholds would be large enough to be discriminated at 4-6 months (Knoblauch et al., 2001). We confirmed in an additional experiment that the colours are discriminable at 4-6 months and that the findings of the current experiment are not related simply to the perceptual similarity of the colours (see Appendix A, figure 7.4). In the current experiment, we used the novelty preference method to look for hue pairs that are distinguished in infant recognition memory, and for hue pairs for which there is no novelty preference despite being discriminable in other contexts. As a second test, we also tested three larger hue pairs which straddled two or more smaller hue pairs to confirm whether or not hues in that region were distinguished in infant recognition memory when chromatic differences were larger. Regions where infants appear to treat hues as if equivalent are identified as being from one hue category, and regions where infants distinguish hues are identified as being categorically distinct.

Systematically mapping infants' hue distinctions, rather than just testing a few 'English' categories as in previous research, avoids a priori assumptions that infant

colour categories align with lexical categories from any one language. Using the

WCS stimulus grid allows direct comparison between the hues distinguished in

infant recognition memory and the lexical distinctions and commonalities present

in the world's colour lexicons, enabling the relationship between infant and lexical

colour categories to be clarified. For example, infant colour categorization is

compared to colour lexicons from the WCS, to identify any correspondence

between the categorical distinctions infants make and those in specific languages.

In addition, we conducted an analysis across all 110 languages in the WCS to see

whether infant colour categories are structured to capture hues that are commonly

central to lexical categories. We then investigated the underlying mechanisms of

infant categorization, and plotted the stimuli and infants' responses in a colour

space which has axes that correspond to the cardinal mechanisms of colour vision

and represent activation along the retinogeniculate pathways.

2.4. Results

2.4.1. Novelty preference and infant colour categories.

Analysis of infant looking times during the familiarization phase confirmed

that infants familiarized to each hue (see Appendix A, Familiarization and Novelty

Preference). Novelty preference scores were calculated as: (time looked at novel

colour during test phase / total time looked at novel + familiar colour during test

phase)*100 (see Appendix A, figure 7.2). Novelty preferences are tested using

Bayesian analysis (Jeffreys, 1961; Kass & Raftery, 1995; Rouder, Speckman, Sun,

Morey, & Iverson, 2009; Wagenmakers, Wetzels, Borsboom, & van der Maas,

2011). Bayes factors are reported which calculate the ratio of how probable the data is given one model (e.g., the null) relative to a second model (e.g., the alternative). A B of 3 or greater indicates substantial evidence for the alternative hypothesis (H1) over the null (H0), often equivalent to $p<.05$ (Jeffreys, 1961). A B of 0.33 or below indicates substantial evidence for H0 over H1 and a B between 3 and 0.33 indicates data insensitivity for distinguishing between either hypothesis. Bayesian analysis is more appropriate for our data than null hypothesis significance testing (NHST) as: i) we require our analysis to enable us to make statements on whether the null hypothesis can be accepted (whether infants treat colours equivalently), whereas NHST provides no measure of credibility in favor of the null and non-significant results do not enable a definite conclusion (Dienes, 2014); ii) we needed a statistical approach which guarantees sensitivity with a minimum number of participants (we have a between subjects design with 16 conditions) and Bayes combined with an optional stopping rule (test until B is sensitive in either direction) enables this as B retains its exact meaning as the evidence in favor of H1 over H0 with further data collection (Rouder, 2014); and iii) Bayes factors should not be adjusted for multiple testing (we have 16 tests) as false alarm rates are dealt with through information in the data with no reference to how many other tests are conducted (Dienes, 2016). In addition to Bayes factors, we report associated p-values from null hypothesis statistical testing (NHST), although these are for reference only since they are affected by the optional stopping rule and multiple testing. We interpret all effects with respect to Bayes factors only.

Stimuli were drawn from row G of the WCS Munsell array (Munsell Value = 4, Y= 12 cd/m^2) in steps of 3 Munsell hues insofar as possible, yielding 14 stimulus hues. The Munsell coordinates of the stimulus hues, preceded by the column number in Figure 2.1, are (2, 5R), (3, 7.5R), (6, 5YR), (9, 2.5Y), (12, 10Y), (15, 7.5GY), (18, 5G), (21, 2.5BG), (24, 10BG), (27, 7.5B), (30, 5BP), (33, 2.5P), (36, 10P), and (39, 7.5 RP).

Starting from column number 3, adjacent sampled hues were paired (e.g., 3&6, 6&9, 9&12……39&2) and novelty preferences for each pair were recorded (see Methods). One-sample t-tests were conducted (against 50%) on novelty preference scores for each pair. Here, *B* refers to a Bayes factor in which the predictions of H1 were modeled as a normal distribution with an SD of 20. All pairs had a sensitive *B* with 10 participants, apart from three pairs (7.5R-5YR, 7.5GY-5G and 5PB-2.5P) which required 17, 20, and 12 participants respectively. Bayes factors revealed support for H1 for four hue pairs: green-yellow (7.5GY-10Y, *t*(9)=4.19, *p*=.002, *B*=686.05; blue-purple (5PB-2.5P), *t*(11)=2.98, *p*=.001, *B*=7.43; blue-green (2.5BG-10BG), *t*(9)=2.81, *p*=.02, *B*=5.05; red-yellow (7.5R-5YR), *t*(16)=2.67, *p*=.02, *B*=3.51; and purple-red (10P-7.5RP), *t*(9)=7.31, *p*=.001, *B*= 4.9E+09 (columns 3-6; 12-15; 30-33; 21-24 and 36-39 in figure 1A). The other 9 pairs showed firm support for H0 (all *B*<1/3, weakest probability of H0 was for pair 7.5GY-5G, where *t*=1.88, *p* =.07, *B*=0.19).

Infants were also tested on three more widely separated stimulus pairs which spanned several of the original pairs (three larger pairs within green, blue, red/yellow). There was firm support for H1 for the large red/yellow pair (7.5RP-10Y, columns 38-12), *t* (9) =2.84, *p*=.02, *B*=6.30E+00 and for H0 for the larger hue

differences within green (7.5GY-2.5BG, columns 24-30) or blue (10BG-5PB,

columns 15-21), (largest t=1.34, smallest p=0.21, largest *B*=0.17). We identify

stimulus 10Y, 2.5Y and 7.5GY as 'yellow' here due to Munsell hue notation,

although at the Munsell value sampled, these hues are darker than prototypical

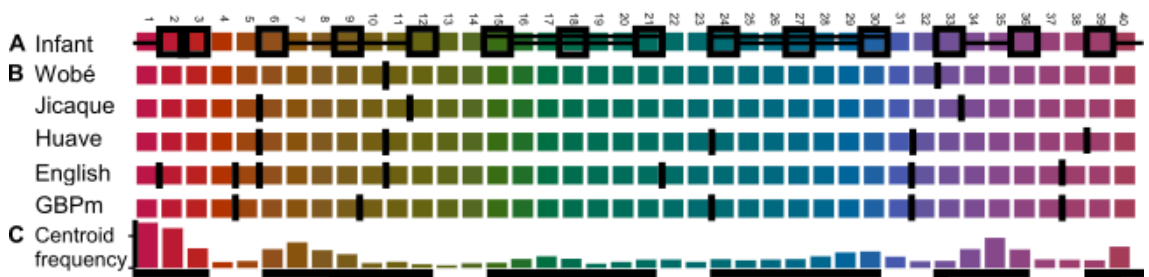yellow. This issue is returned to in the Discussion.

Figure 2.1. Infant colour categorization and the relationship to lexical colour

categorization. (A) Novelty preferences suggest infant recognition memory

distinguishes red-yellow, green-yellow, blue-green and blue-purple hues

but not hues within these categories. Sampled stimuli are outlined in black,

horizontal lines joining stimuli indicate colour pairs which did not elicit

novelty preference, gaps indicate novelty preference. Numbers are from the

WCS stimulus grid and indicate the different hues. (B) Colour naming

systems for row G stimuli based on: WCS data for Wobé (3 Basic Colour

Terms (BCTs)), Jicaque (5 BCTs) and Huave (7 BCTs); English colour

naming (11 BCTs,(Witzel, Sanchez-Walker, & Franklin, 2013); and the

'Green-Blue-Purple' naming motif for row G stimuli (Lindsey & Brown,

2009). Vertical thick black lines indicate category boundaries between

stimuli given the same most frequent term within a language.

Correspondence between the category boundaries in language and infant

novelty preferences can be seen. (C) Frequency of category centroids from

the WCS for each hue in row G (Kay & Regier, 2003). The gaps in the thick

black horizontal bars at the bottom of figure 1C indicate hues which were

straddled by colour pairs which elicited novelty preference, as also shown

by the gaps in the black horizontal lines in figure 1A. Category centroid

frequencies tend to peak in regions which are not distinguished by infant

recognition memory and are generally lowest in regions which are

distinguished.

2.4.2. Relationship to lexical colour categories.

Figure 1B gives examples of colour naming systems for the sampled

stimulus row for a selection of languages from the WCS which illustrate agreement

between infants' response and adult lexical colour categories (Wobé, Ivory Coast;

Jicaque, Honduras & Huave, Mexico) with 3, 5 and 7 basic colour terms (BCTs)

respectively (Regier et al., 2007). Figure 2.1B also gives English naming data from

(Witzel, Sanchez- Walker, & Franklin, 2013) and the green-blue-purple naming

motif (GBPm) that was identified from Lindsey and Brown's (Lindsey & Brown,

2009) cluster analysis of WCS naming data, for row G stimuli. Correspondence

between the distinctions made in infant colour memory and those made by colour

terms and the colour-naming motif can be seen by comparing figure 2.1A and 2.1B.

The 5 categorical distinctions that infants make align with the location of 4 of the

distinctions made in the English colour lexicon, and with lexical distinctions in

colour lexicons with fewer basic terms than English. For example, Huave is a colour

lexicon with 7 basic colour terms and 4/5 of the categorical distinctions in Huave

for row G stimuli are in the same hue region as the distinctions that infants make in

their recognition memory. We show correspondence between infant and lexical

colour categories for a selection of 3 WCS languages, yet inspection of naming data

from the other WCS languages reveals correspondences for many other languages

as well. We also find that infants' categorical distinctions align with 3 of the

categorical distinctions in the GBPm (Lindsey & Brown, 2009).

Figure 2.1C plots the frequency of category centroids in WCS languages for all hues

in row G of the WCS stimulus grid (Kay & Regier, 2003). The plot shows that the

centers of the categories of 110 non-industrialized colour lexicons peak at

particular hues and have minima at particular hues (low centroid counts are likely

to indicate category boundaries). Infant novelty preferences are indicated

underneath the plot by gaps in the solid black horizontal bars. The gaps align

qualitatively well with the low points in the bar plot, corresponding to few WCS

centroids. Distinctions infants make between green-yellow, blue-purple, purple-

red, and red-yellow hues appear to provide fault lines that separate the centroid

peaks from each other (Appendix A, figure 7.3). Infants' distinction between blue-

green hues does not fit so well with this pattern, since although it separates the

centroid peaks at blue and green, it also spans a region of high centroid counts

from WCS languages which have composite blue-green 'grue' terms. Analysis of the

number of category centroids for hues that were straddled by each pair, identified

that the particular combination of 5 pairs for which infants had novelty preference

spanned hues with fewer centroids than 4.27% of any other combination of 5 pairs

from the pairs tested (Appendix A, Analysis of WCS Centroids). This suggests that

hue pairs which are categorically different for infants are in regions which are

infrequently at the center of lexical categories and that infant colour categories are optimally organized around hues which are commonly central to lexical colour categories: fewer than 5% of other 5 pair combinations are better organized.

2.4.3. Underlying mechanisms of infants' response.

To test the hypothesis that infant colour categorization is related to the cardinal mechanisms of colour vision we plotted, using reflectance spectra taken from the University of Joensuu Colour Group database (https://www.uef.fi/en/web/spectral/-spectral-database), the Stockman and Sharpe 2° cone fundamentals (Stockman & Sharpe, 2000) and a D65 illuminant, the stimuli and infants' novelty response in the MacLeod-Boynton chromaticity diagram (MacLeod & Boynton, 1979). In this colour diagram the axes L/ (L+M) and S/ (L+M) represent the 'cardinal' mechanisms of colour vision that correspond to the two main retinogeniculate colour pathways. The results are shown in Figure 2.2.
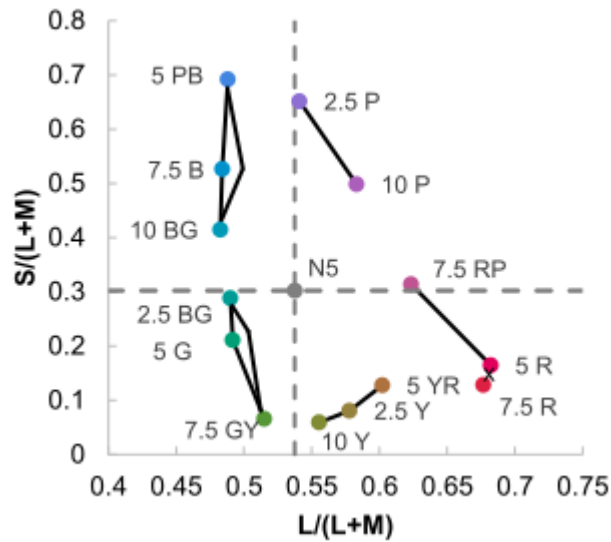
Figure 2.2. Stimuli plotted in MacLeod-Boynton cone-opponent space with (L/
(L+M) and (S/L+M) cardinal axes of colour vision that correspond to the
retinogeniculate pathways. The dashed vertical and horizontal lines
indicate the background (Munsell N5) to which infants were adapted. The
Munsell hue codes for stimuli are given and black lines connecting stimuli
indicate no novelty preference for that pair. The cross between 7.5R and 5R
indicates a pair that was not tested.

A regression analysis found that the Euclidean distances in MacLeod-Boynton
colour space did not predict infants' novelty preferences (R^2 =.01, p=.71, B=2.71E-
17, see also an equivalent analysis in CIELAB colour space in Appendix A
Discrimination and Novelty Preference, and figure 7.4). Inspection of the stimuli
and novelty preferences plotted in the MacLeod-Boynton chromaticity diagram
suggests a relationship with the cardinal colour mechanisms. Four of the pairs for
which there were novelty preferences straddle the vertical and horizontal axes
originating from the background chromaticity, Munsell N5, on which our stimuli
were presented. This indicates a novelty preference in infants when stimulus pairs

are at different polarities (relative to the background) either in S/ (L+M) or in L/ (L+M). Further analyses ruled out the hypothesis that variation in novelty preference across the pairs was driven by a priori preferences (see Appendix A).

2.5. Discussion

Converging evidence from prior research suggests that infants respond categorically to colour. However, since the full hue circle has not been previously tested, the number and location of categorical hue distinctions were unknown. Therefore, the relationship between infant colour categories and those of the world's colour lexicons, and the underlying mechanism of infant colour categories have been unclear. In order to address these issues, we systematically mapped infants' novelty preference responses onto a row of the WCS stimulus grid. Infants successfully familiarized to a given hue, and when presented subsequently with a novel hue, infants had a novelty preference for five pairs of hues in red-yellow, green-yellow, blue-green, blue-purple and purple-red regions of colour space. There was also firm evidence for a lack of novelty response within the hue regions of blue, green, purple, yellow and red. The lack of a novelty response within purple, blue and green regions was found even when the largest hue differences spanning pairs that lacked a novelty response were tested.

As noted earlier, we use the term 'yellow' to denote stimuli in the yellowish region of the hue continuum following the Munsell hue notation. However, stimuli were sampled at constant lightness close to the lightness of the prototypes of other hues but darker than prototypical yellow. The dark and non-prototypical nature of the

stimuli in the yellow region may account for why there was much more individual variation for the less widely separated red-yellow and green-yellow pairs than most other pairs (more infants had to be tested on these pairs for a sensitive Bayes factor), and the novelty preference effect was weakest for the red-yellow pair. Testing these hues at prototypical lightness levels would confirm this. Nevertheless, whatever the appropriate gloss for the yellowish hues (and this would obviously vary across languages), the current study identifies a categorical distinction for infants in this region.

An additional experiment and further analysis ruled out the hypothesis that novelty preferences were simply related to perceptual similarity and confirmed that colours can be discriminated in other contexts (see Appendix A, Discrimination and Novelty Preference). The findings therefore suggest that infants' recognition memory is categorical: some colours are treated as if they are equivalent in infants' recognition memory, yet others which are not always more perceptually dissimilar are treated as if they are different. Overall, our findings suggest that infant memory parses the hue continuum at the lightness level tested into five categories: red, yellow, green, blue and purple. Prior research has provided evidence that infants' recognition memory parses colour into blue, green (Bornstein et al., 1976; Catherwood, Crassini, & Freiberg, 1987; Clifford et al., 2009; Franklin & Davies, 2004) and purple (Franklin & Davies, 2004) categories, with a suggestion of separate red and yellow categories as well (Bornstein et al. 1976). Unlike prior studies, we systematically sampled at regular intervals around the complete hue circle, providing the first evidence that infant memory also distinguishes purple and red.

2.5.1. Relationship to lexical colour categories.

       Mapping infant categories onto the WCS stimulus grid clarifies the relationship between infant colour categories and lexical colour categorization. Correspondences between the location of infants' categorical distinctions and those in colour lexicons can be seen. In particular, the common green-blue-purple naming motif that was revealed by Lindsey and Brown's (Lindsey & Brown, 2009) cluster analysis of WCS data has categorical distinctions in four of the same hue regions as those of infants. This correspondence between the distinctions that infants make and those in colour naming systems is also highlighted by our comparison of infant colour categories and the locations of the WCS category centroids from Kay and Regier (Kay & Regier, 2003). Infants have separate red, yellow, green, blue and purple categories, and there are also separate clusters of category centroids from WCS languages in these hue regions. Infants' categorical distinctions isolate the peaks in category centroids from one another. An analysis revealed that hues at infant colour category boundaries are not commonly at the center of lexical colour categories. This suggests that hues within infant colour categories (hues straddled by pairs where we find no novelty preference) are commonly at the center of lexical colour categories. Infants' blue-green categorical distinction did not fit the pattern so well, since it fell in a region where there are a high number of lexical category centers due to the high incidence of WCS languages with a composite green-blue 'grue' term. Nevertheless, that fewer than 5% of other 5 pair combinations were better organized around hues which are commonly central to lexical colour categories, does indicate a striking similarity between pre-linguistic and lexical categorization.

2.5.2. Underlying mechanisms.

We found no evidence that infants' novelty preference is driven by how perceptually similar hues are. However, when infants' novelty response was plotted in a colour space defined by the cardinal colour sub-systems that correspond to the retinogeniculate pathways underlying colour vision, we see for the first time that four of the categorical distinctions that infants make are separated by axes in this colour space that pass through the chromaticity of the background, which could be considered the 'adaptation point'. We propose therefore that the null points of the two cardinal subsystems of colour vision provide boundaries that infants may use to parse the colour continuum into categories in their recognition memory. This of course cannot account for infants' categorical distinction between red and yellow – which must derive from alternative mechanisms.

Our proposal that the cardinal colour mechanisms provide fault lines for infant colour categorization is related to similar arguments made about adult colour naming. For example, one study of adult colour naming and hue settings provides evidence that the cardinal axes align with adults' blue-green and yellow-green category boundaries (Malkoc, Kay, & Webster, 2005). Another study suggests that whether or not L-M cone-contrast between the colour and background is positive (reddish) or negative (greenish) aligns with a common categorical distinction in WCS languages between warm and cool colours (Xiao et al., 2011). Similarly, we also find that whether or not colours are 'redder' or 'greener' than the background

(values higher and lower than the background on the L/(L+M) axis) provides a fault line for infants' green-yellow and blue-purple categorical distinctions, but we also find that S/(L+M) provides a fault line for infants' red-purple and blue-green categorical distinctions. A link between low-level mechanisms of colour vision and categorization is also implied by a computational simulation which shows that universal colour categorization can be accounted for by human's just noticeable difference function (Baronchelli et al., 2010; Mullen & Kulikowski, 1990). It has been suggested that categorical clustering of neurons at V1 can account for the warm/cool categorization in languages (Xiao et al., 2011). However, an association between the cardinal mechanisms and categorization does not necessarily indicate that neurons code categorically at early stages of the visual system. The cardinal mechanisms may simply provide perceptual inequalities which provide a basis for post-perceptual categorization in temporal and frontal regions of the brain (Brouwer & Heeger, 2013; He et al., 2014; Koida & Komatsu, 2007; Persichetti et al., 2015).

Although we point to an association between the cardinal mechanisms of colour vision and infant colour categorization here, it is clear that in addition to such biological forces, culture, environment and communication are likely also to determine both how many colour terms there are in a lexicon and the categorical distinctions that are needed. It seems likely that languages would override categorical distinctions that are important in infant colour memory if they are not relevant for a given culture or environment (Hespos & Spelke, 2004). One important question for further research is how we transition from a pre-linguistic colour categorization based largely on biological mechanisms to a lexical colour

categorization that may make additional or fewer distinctions. The lack of one-to-one mapping between pre-linguistic and lexical colour categorization may well partly explain the difficulty that children have in learning the words for colours (Franklin, 2006; Johnson, McQueen, & Huettig, 2011; Pitchford & Mullen, 2003; Wagner, Dobkins, & Barner, 2013). Further research should also examine whether the distinctions in infant colour memory are 'universal' across different cultures and environments. Given the link to the cardinal mechanisms of colour vision we expect them to be largely consistent across cultures, but cultural variation in pre-linguistic categorization is at least theoretically possible.

To conclude, we find that infant recognition memory parses the hue circle into blue, green, purple, yellow and red categories, and we find similarity in the structure of pre-linguistic and lexical colour categorization. The retinogeniculate mechanisms of colour vision appear to provide fault lines for infants' categorical distinctions between hues. Our findings provide further evidence that colour categorization has biological origins. Our results also relate to broader debate on the biological origins of aspects of cognition such as knowledge about the physical world, mathematical ability and spatial cognition (Hespos & Spelke, 2004). Although certain cognitive processes may seem to a large extent to be culturally or linguistically constructed due to apparent linguistic and cultural diversity, by looking at commonalities across cultures and languages, and by investigating these cognitive processes in infancy, biological origins of cognitive processes can also be revealed.

2.6. Methods

2.6.1. Participants

A total of 295 4-6 month old infants took part in the study, with 116 infants excluded from the final sample for the following reasons: infant fussiness or lack of looking (N=78); family history of colour vision deficiency (N=3); failure to familiarize during the familiarization phase, as defined by a non-negative slope of looking times across familiarization trials (N=17), failure to look during the test phase (N=12), equipment or experimenter error (N=3), prematurity (N=3). The final sample of 179 infants (89 males) had a mean age of 21.3 weeks (SD 2.42). All infants had a birth weight greater than 2500g and no known visual or neurological conditions. Ethical approval for this study was obtained from the Sciences and Technology cross schools ethical committee at University of Sussex, and the European Research Council Executive Agency ethics committee. Written informed consent was obtained from the parents of the participants

2.6.2. Apparatus.

Stimuli were presented to infants in two square 12 x 12 cm windows of a wooden booth painted with gray Munsell N5 paint (Y=19.77 cd/m^2, x=0.312, y=0.325). The two stimulus windows were 3.5 cm to the left and right from central fixation, and the infant was sat in a car seat at eye-level to the horizontal center of the windows at a distance of 50 cm. A 4 by 5 cm digital display was embedded into another window at the central fixation point in order to centrally fixate infants in

between trials, and a circular hole above this (diameter = 2cm) had a webcam

positioned behind it focused on the infants' face. A pulley system around the back

of the booth allowed the left and right stimulus windows to either display stimuli

during trials, or two squares of Munsell N5 gray and the central digital display

during inter-trial intervals. The webcam fed into a computer (Dell Precision 390),

which recorded the infants' faces in QuickTime. A Matlab program indicated the

onset and offset of trials and allowed coding of infant looking. Stimuli were viewed

under a D65 illuminant (X-Rite**:** Judge II (6500K) 24"), with a D65 bulb embedded

in a hood at the top of the booth and two D65 spot lights angled directly onto the

two stimulus windows from behind the infant in order to ensure the appropriate

amount of light was reflected from the stimuli. There was no other light source in

the room and the room had black walls and no windows.

Stimuli were sampled from the WCS stimulus array: an array of 320 colours from

the Munsell system that vary in Munsell value (lightness) and hue and are at

maximum chroma (similar to saturation or colorfulness) for each given stimulus.

Stimuli were sampled from row G of the array (Munsell value = 4, Y= 12 cd/m^2) in

steps of 3 Munsell hue, giving 14 hues in total (5R, 7.5 R, 5 YR, 2.5 Y, 10 Y, 7.5 GY, 5

G, 2.5 BG, 10 BG, 7.5 B, 5 PB, 2.5 P, 10 P, 7.5 RP). Stimuli were presented as squares

(12 cm for infants) of reflective Munsell card.

2.6.3. Design and Procedure.

Infants were tested with a novelty preference procedure, where there was a familiarization phase with one hue repeatedly shown, and then a test phase where the familiar hue was paired with a novel hue across four trials. The time spent looking at the novel hue relative to the test hue during the test phase was calculated (novelty preference). Each infant saw one hue pair, and there was a minimum of 10 infants per pair (infants randomly allocated), with the hue that was familiar or novel counterbalanced for each pair. Hue pairs were defined first by pairing adjacent stimuli separated by 2 Munsell hue units. Where there was no novelty preference for two or more adjacent hue pairs then the larger hue difference spanning the adjacent pairs formed another hue pair to be tested. During the familiarization phase the same hue was presented in left and right windows for 8 8-second trials, and in the test phase one familiar and one novel hue were presented for 4 5-second trials with the left/right location of the novel hue counterbalanced and randomized. Inter-trial intervals were a minimum of 1 second and the trial then commenced once infants were centrally fixated, with a minimum 2-second interval between the familiarization phase and the test phase. An experimenter sat behind the infant testing booth worked the pulley system to reveal the stimuli during each trial and to reveal, during the intertrial intervals, the digital display which played a black and white looming and contracting bulls-eye central attention getter. A second experimenter viewing the webcam output coded infant looking online, while blind to the condition (colours tested) and location of the novel colour. A subset (21%) of the data was coded twice, by an independent

experimenter blind to condition and stimulus location, giving an inter-rater

reliability of Pearson's r=0.91.

Chapter 3 - Paper 2: Infants look longer at colours that adults like when colours are highly saturated.

Skelton, A. E., & Franklin, A. *Psychonomic Bulletin* (submitted)

3.1. Abstract

The extent to which aesthetic preferences are 'innate' has been highly debated (Reber, Schwarz, & Winkielman, 2004). For some types of visual stimuli infants look longer at those that adults prefer. It is unclear whether this is also the case for colour. A lack of relationship in prior studies between how long infants look at different colours and how much adults like those colours might be accounted for by stimulus limitations. For example, stimuli may have been too desaturated for infant vision. In the current study, using saturated colours more suitable for infants, we aim to quantify the relationship between infant looking and adult preference for colour. We take infant looking times at multiple hues from a study of infant colour categorisation (Skelton, Catchpole, Abbott, Bosten, & Franklin, 2017), and then measure adult preferences and compare these to infant looking. When colours are highly saturated, infants look longer at colours that adults prefer. Both infant looking time and adult preference are greatest for blue hues and are least for green-yellow. Infant looking and adult preference can be partly summarised by activation of the blue-yellow dimension in the early encoding of human colour vision. These findings suggest that colour preference is at least partially rooted in the sensory mechanisms of colour vision, and more broadly that aesthetic judgements may in part be due to underlying sensory biases.

3.2. Introduction

It is well established that humans have preferences for some visual stimuli over others, for example, preferences for specific faces, patterns, colours or spatial compositions (e.g. Fancher, 1996; Palmer & Schloss, 2010; Rhodes, Hickford, & Jeffery, 2000). The source of these perceptual and aesthetic preferences is much debated (e.g. Ramachandran & Hirstein, 1999; Reber et al., 2004). One idea is that preferred visual stimuli have characteristics that are optimal for the human visual system to process, and therefore that these preferences are to some extent 'innate' (Krentz & Earl, 2013; Ramachandran & Hirstein, 1999). In support of this idea there is evidence that infants look longer at visual stimuli that adults prefer. For example, infants look longer at attractive than unattractive faces, both human (Damon, Mottier, Meary, & Pascalis, 2017) and non-human (Quinn, Kelly, Lee, Pascalis, & Slater, 2008), and longer at patterns with vertical than horizontal symmetry or asymmetrical patterns which are less preferred by adults (Bornstein, Ferdinandsen, & Gross, 1981). Infants also look longer at original art that adults prefer than art where the balance or focus has been altered (Krentz & Earl, 2013). However, in the case of colour preferences, the relationship between infant looking and adult preference is less clear.

Colour preference might seem to be a personal and idiosyncratic phenomenon. However, studies have repeatedly found a consistent pattern of colour preference in adults: on average, preference ratings follow a smooth curve as colours vary in hue, with a preference maxima at blue, a minima at dark yellow, and with cool colours generally preferred over warm colours (Hurlbert & Ling, 2007; Palmer &

Schloss, 2010). This pattern of colour preference has been measured as far back as 1897 (Jastrow, 1987), and the broad pattern of preference is generally consistent across industrialised cultures (but see Taylor, Clifford, & Franklin, 2013 for an example of cultural variation). Various theories of colour preference have argued that patterns of colour preference are in some way 'natural and universal' and that at least some aspect of colour preference is 'innate'. For example, Ecological Valence Theory (EVT, Palmer & Schloss, 2010) proposes that people like/dislike colours to the extent that they like/dislike the objects that are associated with the colours. Whilst such associations can be learnt during an individual's lifetime, EVT also suggests that innate colour preferences could draw humans to entities which are evolutionary beneficial (e.g., clean water) and away from those which are not (e.g., rotting waste). Others (e.g., Hurlbert & Ling, 2007) have highlighted how patterns of colour preference can be effectively summarised in terms of the two fundamental neural dimensions that underlie early colour encoding (the 'red-green' and 'blue-yellow' cone-opponent processes), perhaps suggesting that these colour preferences are rooted in the basic mechanics of the visual system rather than higher level conceptual thought.

Further weight to claims of the 'innateness' of colour preference would be given if a relationship between infant looking and adult colour preference was established. Several studies have found that infants look longest at blue hues and least at yellow or yellow-green (Adams, 1987; Bornstein, 1975; Franklin, Bevis, Ling, & Hurlbert, 2010; Franklin, et al., 2008; Teller, Civan, & Bronson-Castain, 2004; Zemach, Chang, & Teller, 2007), these maxima and minima in looking times do broadly correspond respectively to adults' highly liked and disliked colours (e.g.

Taylor, Schloss, Palmer, & Franklin, 2013; Hurlbert & Ling, 2012). However, other

studies have found a less favourable correspondence. In one study, infants were

found to look longer at yellow than blue (Adams, 1987). One reason for

discrepancies between infant and adult studies could be the differences in

lightness and saturation of stimuli across studies, as hue preferences interact with

lightness and saturation (Palmer & Schloss, 2010; Camgoz, Yener, & Guvenc, 2002).

Only two studies have tested infants and adults using the same stimulus set. One

study tested eight colours that were radiant and monochromatic lights (untypical

of natural surfaces) and found that infants generally looked longer the more adults

liked a colour (Bornstein, 1975). Another study tested only four hues at two

lightness and saturation levels, and found no relationship between infant looking

time and adult preference (e.g., infants did not look longer than chance at blue

hues) (Taylor, Schloss, Palmer, & Franklin, 2013). However, stimuli were

relatively desaturated, and it is possible that the discrepancy between infants and

adults was due to infants' poor discrimination of blue-yellow differences (tritan

colour vision) at low saturation (e.g., see Teller, Brooks, & Palmer, 1997), and that

a stronger relationship between infant and adult measures would exist at higher

saturations.

In the current study, we aim to establish whether infants do look longer at colours

the more adults like them by using a more comprehensive and suitable stimulus

set than prior studies. We reanalyse data from a study of infant colour

categorisation (Skelton, Catchpole, Abbot, Bosten, & Franklin, 2017) to obtain

infant looking times for various hues, and measure adult preferences for these

same hues. Skelton et al.'s infant study investigated colour categorisation (not

preference) using a novelty preference method where 4-6 month old infants were first familiarised to one hue and then shown a novel hue, and separate groups of infants were tested on 13 different hue pairs. Here, in order to identify infants' pattern of colour preference, we analyse the length of time infants spent looking on the first trial of the familiarisation phase, giving looking times for 14 hues. We analyse the first trial of familiarisation rather than the total looking time across all 8 familiarisation trials since differences between stimuli are likely to wash out over time as infants habituate to stimuli (as is required for the novelty preference method). Hues were reflective stimuli that are more typical of surfaces in the natural world than computer rendered or light based stimuli, were at a constant lightness level and were at or close to the highest saturation levels for each given hue. Based on prior studies of infant colour vision (e.g., Knoblauch, Vital-Durand, & Barbur, 2001), it is anticipated that 4-6 month old infants would be able to easily detect all stimuli, and that both red-green and blue-yellow discriminations could be made at such high saturation levels. We relate infant looking times to these hues to adult ratings of colour preference. We also relate both measures to how the hues activate the 'red-green' and 'blue-yellow' dimensions of colour encoding (as done for adults in Hurlbert & Ling, 2007, and infants in Franklin, Bevis, Ling, & Hurlbert, 2010), to identify the extent to which infant looking time and adult preference can be summarised by basic sensory processes that underpin colour vision.

3.3. Method

3.3.1. Participants

3.3.1.1. Infants

Data from 295 4-6 month old infants who took part in a study on colour

categorisation in infants (Skelton et al., 2017) was analysed. The final data set

consisted of 201 infants (97 male, M_{age} = 21.23 weeks, SD= 2.47), as 94 infants were

excluded for the following reasons: fussiness (n=78), lack of looking during the

critical first trial (n=7), family history of colour deficiency (n=3), prematurity

(n=3), and experimenter or equipment error (n=3). All infants were full term,

weighed over 2500g at birth, and had no known neurological or visual conditions,

and parents reported no family history of colour deficiency.

3.3.1.2. Adults

Forty adults (5 males) from the University of Sussex ($M_{age=}$ 20.63 years, SD=

3.21) took part. All participants were screened for colour vision deficiency using

Ishihara's test for colour deficiency (Ishihara, 1917).

3.3.2. Stimuli and set up

The colours were sampled from the World Colour Survey stimulus array, a

set of 320 colours in the Munsell system which vary in Munsell value (lightness),

hue, and are at high chroma (similar to colourfulness, or saturation) for each

stimulus. Stimuli were 14 hues sampled at regular intervals of Munsell hue around the colour circle at one lightness level (Munsell value 4, Y= 12cd/m^2).

In the Munsell system hues are divided around the hue circle into hue sectors: red, yellow-red, yellow, green-yellow, green, blue-green, blue, blue-purple, purple, and red-purple, using initials (R, YR etc.) for simplicity. The Munsell notation of the stimuli is given in the form: hue value/chroma. The full notations of stimuli are; 5 R 4/14, 7.5 R 4/14, 5 YR 4/8, 2.5 Y 4/6, 10 Y 4/6, 7.5 GY 4/8, 5 G 4/10 2.5 BG 4/8 10 BG, 4/8, 7.5 B 4/8, 5 BP 4/10, 2.5 P 4/10, 10 P 4/10, 7.5 RP 4/10. Stimuli are also plotted here in a version of the MacLeod Boynton chromaticity diagram (figure 3.1), where the two axes represent activation in the retinogeniculate pathways that underlie colour vision L/(L+M) ('red-green') and S/(L+M)) ('blue yellow'). The conversion of stimuli from CIE xyY to the MacLeod Boynton Chromaticity Diagram was carried out with reflectance spectra taken from the University of Joensuu Colour Group database (https://wwww.ue.fi/en/web/spectral/spectraldatabase), the Stockman and Sharpe 2° cone fundamentals (Stockman & Sharpe, 2000), and a D65 illuminant.
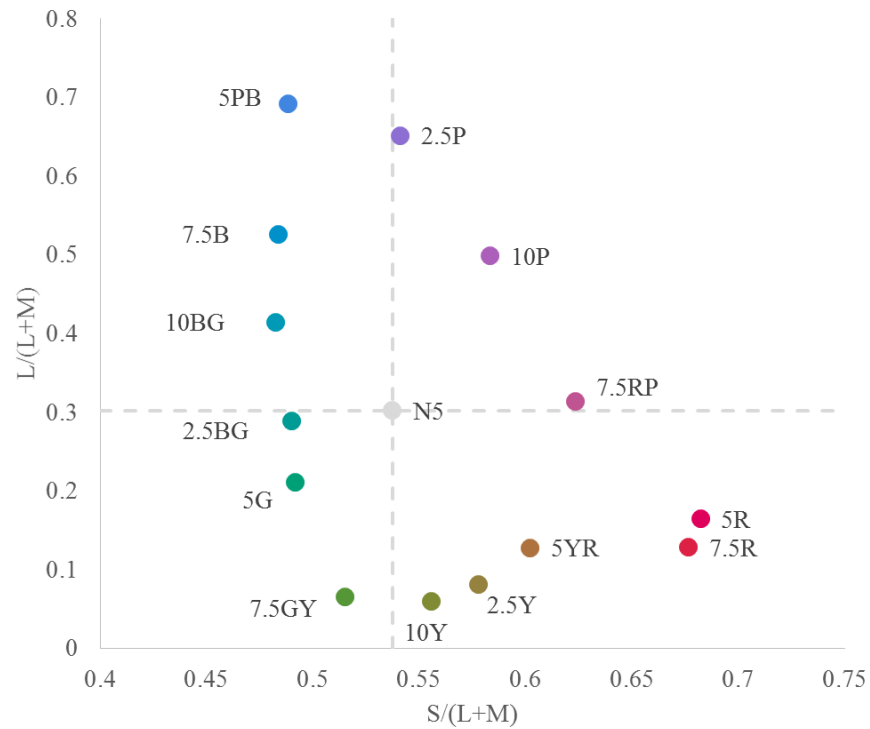
Figure 3.1. Stimuli plotted in MacLeod-Boynton cone-opponent space with

(L/(L+M) and (S/L+M) cardinal axes of colour vision which correspond to

activation of the retinogeniculate pathways. The dashed vertical and

horizontal lines indicate the background (Munsell N5) to which infants and

adults were adapted. The Munsell hue codes for stimuli are given.

For the infants, colours were presented as two 12cm squares in a viewing booth

painted with Munsell N5 paint (Y= 19.77 cm/m^2, *x*=0.312, *y*=0.325). The stimuli

were presented in two windows whose inner edge was 3.5cm to the left and right

of central fixation. Infants were seated in a car seat 50cm away from the centre

point of these windows. Colours were illuminated by an overhead illuminant and

by two spotlights angled onto the stimuli from behind the infant. All lighting was

an artificial simulation of natural daylight illumination (D65, 6500k).

Adults' stimulus colours were identical to those used in the infant experiment.

Each colour was presented as a 5 cm square mounted on card painted with

Munsell N5 paint. A table was set up in the infant testing booth allowing adult

participants to view the colours under the same illumination condition as the

infants.

3.3.3. Design and Procedure

Infant data is taken from the looking times in Skelton et al.'s (2017) colour

categorisation study. Here, for the purpose of examining colour preference, the

looking time from the first 8 second trial in Skelton et al. is analysed. In Skelton et

al., prior to the first trial, infants were centrally fixated with a black and white

looming attention-getter displayed on a small screen between the two windows of

the booth. Once the attention-getter was centrally fixated, two identical squares of

colour were lowered into the viewing windows, and an experimenter blind to the

condition coded infant looking to the colours using a MATLAB program whilst

viewing the infant via a webcam. Each infant saw one hue, and there was a

minimum number of 10 infants per hue, with infants randomly allocated to each

hue. Skelton et al. followed an optional stopping procedure that is routine when

using Bayesian analysis. This means that the sensitivity of the Bayes Factors in the

analysis of Skelton et al. determined how many infants were tested: testing

stopped when a sensitive Bayes Factor was reached in support of either the null or

alternative hypotheses (e.g., Rouder, 2014). As a result of this the number of

participants allocated to each hue are not equal across hues (average N per pair = 14.35, SD = 4.52).

Adults were shown colours individually in a random order twice and were asked to rate their preference for the colours on a scale ranging from 0 to 100 by making a mark on the line that represented the scale.

3.4. Results

As in Skelton et al., traditional null hypothesis significance testing is accompanied by Bayes factors to aid with the interpretation of the data. Bayes factors allow richer interpretation of the strength of the evidence for either the null or alternative hypothesis, (Dienes, 2014), and in the case of regression they allow us to assess the predictive strength of each possible regression model, without having to correct for multiple comparisons, a process which can increase the chance of type II errors (Dienes, 2016). A BF of 0.33 indicates evidence for the null hypothesis, and a BFBF of 3 and above indicates substantial support for the alternative hypothesis. Values close to 1 suggest that the data is not sensitive enough to concretely support either the null or alternative hypothesis (Wetzels & Wagenmakers, 2012).

3.4.1. Comparison of infant looking time and adult preference ratings

Total infant looking times to both left and right squares of colour were averaged across infants for each hue. Infants looked for longest at one of the blue hues (10 BG, *M*= 4236ms, *SD*= 1180.31), twice as long as the hue they looked at least, which was one of the yellow hues (2.5 Y, *M*= 1996 ms, *SD*= 1239.60). Adults maximum and minimum preference ratings were for the same hues that infants looked lonest and least at, with the highest preference for 10 BG (*M*= 78.86, *SE*= 2.52), and lowest for 2.5Y (*M*= 18.02, *SE*= 2.11), (figure 3.2). As can be seen in figure 3.2, infants tend to look longer the more adults prefer the colour. This was confirmed with by a significant robust correlation (using the MATLAB toolbox, Pernet, Wilcox, & Rousselet, 2003)**,** between infant looking time and adult preference ratings across hues, *r*=0.73, *t*= 3.707, *p*= 0.003, bootstrapped 95% CI [0.39 0.91], BF= 17.73.
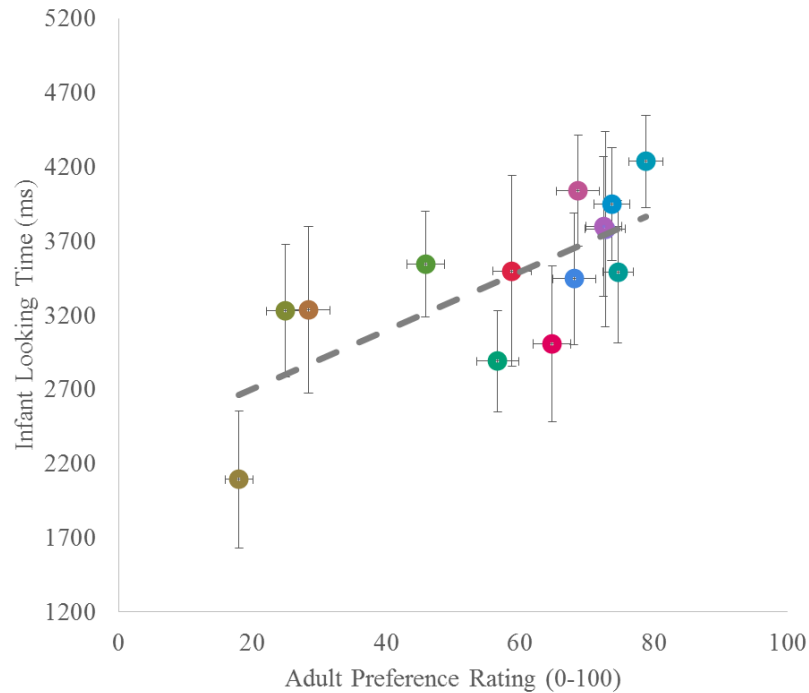
Figure 3.2. Correlations between average infant looking time (ms) and average

adult preference rating (0-100). Error bars +/- 1SE

3.4.2. Sensory mechanisms of colour preference

In order to assess whether the sensory mechanisms that underpin colour

vision could summarise infant looking times or adult colour preference, a series of

regression analyses were conducted. To determine which model, $L/(L+M)$ or

$S/(L+M)$, or a combination of both, is most accurate at predicting infant and adult

response to colour, a stepwise regression with $L/(L+M)$ entered first and $S/(L+M)$

second into the model as predictor variables for infant looking time and adult

preference. Bayes Factors were calculated using an R package, BayesFactor,

(Rouder & Morey, 2012, Liang, Paulo, Molina, Clyde, & Berger, 2008) for all

possible models. The stepwise regression found that a significant amount of the

variance in infant looking time could be predicted from S/(L+M) alone, with infants looking for longer at colours which were bluer (greater S/(L+M) activation), R^2= 0.304, $F(1,12)$= 5.23, p= 0.041, Beta= 0.551 (figure 3.3). However, the BF for this model was 2.02, suggesting there is not firm evidence in this dataset for the experimental hypothesis (Bayes factors for both L/(L+M) and L/(L+M) & S/(L+M) models were also insensitive, BF= 0.54, BF=0.97 respectively).

For adults, the stepwise regression also found that the best model was S/(L+M) alone, and adults preferred colours more which were bluer (greater S/(L+M) activation), R^2=0.515, F= 12.76, p=0.004, Beta=0.718, BF= 10.41 (figure 3.3). Note, the Bayes Factor for a model with both L/(L+M) and S/(L+M) was 4.14, demonstrating that a model with both predictors would also predict variation in adult preference ratings, although to a lesser extent than S/(L+M) alone.
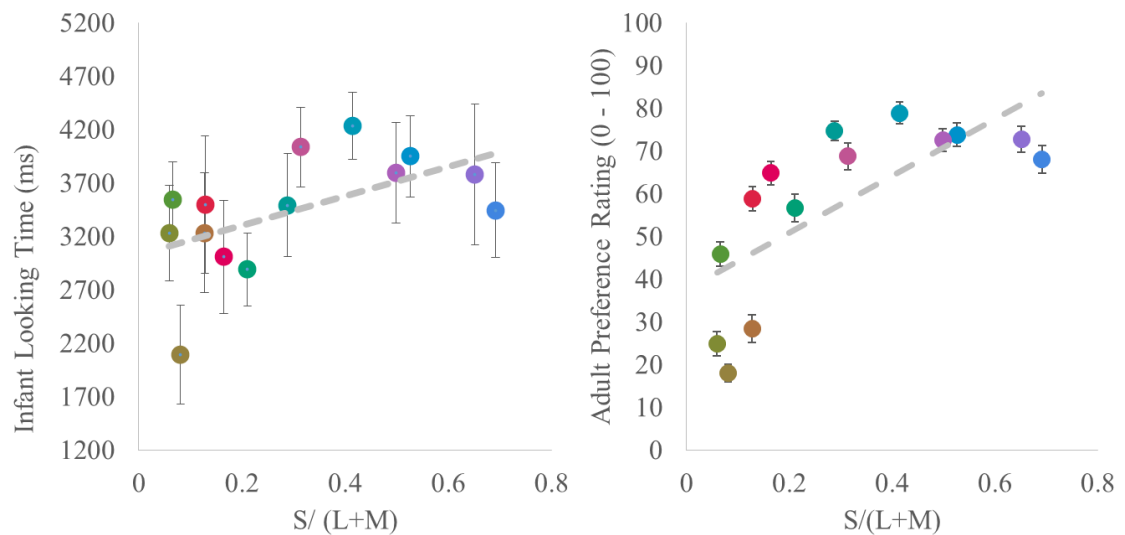

Figure 3.3. Correlations of average adult preference rating (0-100) and S/(L+M) (left), and average infant looking time (ms) and S/(L+M) (right). Error bars +/- 1SE.

3.5. Discussion

The current study aimed to quantify the relationship between how long infants look at colours and how much adults like those colours. We found a striking correspondence between infant looking and adult liking. The colour looked at least by infants was the most disliked by adults and the colour looked at most by infants was the most liked by adults. The relationship between infant and adult measures was significant and infant looking times accounted for over half of the variance in adult preferences. Infant looking and adult preference were also both best accounted for by a sensory model of colour vision which quantified how the colours activate the 'blue-yellow' S/(L+M) retinogeniculate pathway.

The pattern of infant looking across colours, where infants look longest at blue hues and least at yellow/green hues was similar to several prior infant studies (e.g. Bornstein, 1975; Franklin et al 2010, Franklin , et al., 2008; Teller, Civan, & Bronson-Castain, 2004; Zemach, Chang, & Teller, 2007; see also Brown & Lindsey, 2013). The current study elaborates on the pattern of infant looking by using a far more extensive stimulus set than in prior studies. The stimulus set in the current study also had colours that were well above infant chromatic thresholds at 4-6 months and which were at very high saturation levels to guard against the concern that infants cannot make tritan discriminations at low saturation. Given the correspondence between infant looking and adult liking in the current study when stimuli are at high saturation, we propose that the different pattern of infant looking and lack of infant and adult correspondence in Taylor et al. 2013 was due to stimuli being de-saturated.

Adult colour preferences, and to a lesser extent infant looking times at colours could be effectively summarised by the underlying sensory mechanisms of colour vision. The fact that S/(L+M) along was the best predictive model of both infant looking and adult preference provides further weight to the argument that infants and adults have a similar pattern of response to the colours. Previous studies, also report that adults give a positive weighting to S/(L+M), with adults rating more blueish hues as more preferred (Hurlbert & Ling, 2007), although one prior study found that infant looking is best summarised by L-M (Franklin et al., 2010). We propose that this discrepancy can again be explained by infants' poor tritan discrimination at low saturation levels – when stimuli are highly saturated as in the current study and unlike in Franklin et al., 2010, S/(L+M) is the strongest predictor of infants' response just like for adults. For both adults and infants, the relationship between S/(L+M) and their response does appear to be somewhat curvilinear (with their response peaking at blue not at maximum S/L+M) which explains why a simple linear model of sensory mechanisms only predicts around half of the variance in response. More complex modelling of other colour spaces may capture infant colour preferences better than just cone-opponency, as in adults (Schloss, Lessard, Racey, & Hurlbert, 2017). Nevertheless, the relationship of adult colour preference with S/(L+M) and also with infant looking times provides further weight to the argument that colour preference is at least partially rooted in the sensory mechanisms of our colour vision.

Of course, how long infants look at colours cannot completely account for how much adults like colours – just over half of the variance in adult preference is explained. This leaves room for other experiential factors to contribute to adult

colour preference such as the associations between colour and objects that are made over a lifetime (e.g., Palmer & Schloss, 2010). We are not suggesting that colour preferences are completely 'innate'. We also do not suggest here that how long an infant looks at a colour reflects their affective or aesthetic response to colour. Infants might look longer at stimuli for reasons other than liking those stimuli. For example, novelty or complexity is known to drive infants' looking response, for example infants look for longer at a fearful face than a happy face (Peltola, Leppanen, Palokangas, & Hietanen, 2007). Adults do look longer at stimuli that they like (Taylor et al., 2010), yet we are unable to determine from this and prior studies whether this is the case for infants (see Taylor et al., 2010 for further discussion of this issue). Further research which aims to identify how infants' sensory biases to some colours over others matures into a conscious and explicit affective response to colour is needed. For now we establish that when colours are sufficiently saturated for infants to see there is a high degree of similarity between how long infants look at those colours and how much they are liked by adults.

Chapter 4. Further investigation of the Munker- White illusion in infancy

Skelton, A. E., & Franklin, A, *Infant Behaviour and Development* (under review)

4.1. Abstract

Investigating whether the developing visual system perceives visual illusions can further understanding of how low-and high-level perceptual processes develop, and also of the mechanisms behind the illusions. A previous study (Yang, Kanazawa, & Yamaguchi, 2010) suggested that 4-8 month old infants can perceive the Munker-White illusion, an illusion where colours appear different depending on their context. Here we question whether the illusory effect of Yang et al.'s stimuli really would be strong enough for 4 month old infants to detect given their poor chromatic sensitivity. In Experiment 1, we attempt to replicate Yang et al's study, and in Experiment 2 we adopt an alternative habituation method. Neither experiment provides evidence that infants at 4 months perceive the Munker-White illusion. The methodological challenges in establishing whether or not infants perceive visual illusions are discussed.

4.2. Introduction

4.2.1. Visual illusions in infancy

Visual illusions are a by-product of the visual system trying to understand ambiguous information, and are a key feature of perceptual experience (Corney & Lotto, 2007). Research on the perception of illusions in infancy could potentially provide a greater understanding how perceptual experience develops, how equivalent infant and adult perception is, as well as the mechanisms behind the illusion itself (Pereverzeva & Teller, 2009). Prior studies have argued that infants perceive illusions that depend on visual completion and illusory contours, such as the Kanizwa square (Kawabata, Gyoba, Inoue, & Ohtsubo, 1999), simultaneous contrast (Pereverzeva & Teller, 2009) and the Munker-White illusion (Yang et al., 2010). If infants really do perceive these illusions then it suggests that the visual processes that underpin these illusions such as assimilation, perceptual transparency, and figure-ground processing are active in early infancy. The current study re-visits the claim that infants perceive the Munker-White illusion. We provide both a replication and extension of prior research in order to establish whether infants really do perceive this illusion and to further understand how the illusion works.

4.2.2. The Munker-White illusion

The Munker-White illusion is an illusion where a colour is perceived as different depending on the context. (White, 1979) The illustration in figure 4.1

shows the same orange coloured circle either on a blue background with green

overlapping stripes (on the left), or on a green background with blue overlapping

stripes (on the right). Both left and right circles are composed of the same orange

colour (as in the top central circle), yet the context of the stripes and background

means that the orange is perceived differently in the two examples. Theories on

the illusion have previously suggested the involvement of low-level mechanisms

such as colour assimilation (Ripamonti & Gerbino, 2001) and simultaneous

contrast (Anderson , 2003). Colour assimilation is a colourimetric shift towards a

surrounding colour, and simultaneous contrast is a colourimetric shift away from a

surrounding colour. However, models incorporating *only* these low-level

mechanisms can underestimate the size of the illusion in adults. It is only by

including higher-order processes as well that the illusion can be accounted for. For

example, by including scission; the segmentation of a scene which presumes the

illusory colour is an object which lies between the foreground and background

(Anderson, 2003).
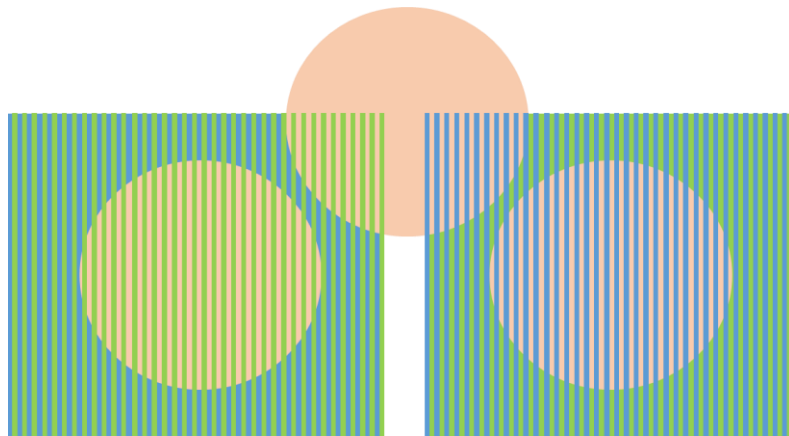

Figure 4.1. Illustration of the Munker-White illusion. There are a total of three

individual chromaticities in this image, the stripes (blue and green), and the

circles (orange). All three circles in the image are composed of the same

orange colour but are perceived as different depending on the surround and foreground (e.g. on a blue background with green stripes in the foreground (left), or on a green background with blue stripes foreground (right)).

There is evidence that the low-level processes that have been implicated in the Munker-White illusion are present from 4-6 months old. For example, Pereverzeva and Teller, (2009), demonstrated simultaneous colour contrast in infants at 4 months. They presented infants with two coloured circles; one embedded in a static chromatic surround, and the other in a temporally modulating surround which flickered between two chromaticities at a rate below threshold for adults. As it was below threshold, it was perceived as static, but the modulation of colour resulted in the embedded circle being perceived as shifted in colour a result of simultaneous contrast between stimulus and surround. Infants preferred the modulating stimulus over the static, showing that they could detect the changes in the chromaticity of the embedded circle. Higher order scene segmentation abilities such as scission have also been shown to be present in infants 4-7 months old (e.g., Johnson & Aslin, 2000). Johnson and Aslin (2000) habituated infants to a stimulus where a coloured rod moved behind a semi-transparent rectangle which altered the hue of the part of the rod which it overlapped. Infants at test looked preferentially at a two coloured rod, rather than a single coloured rod, suggesting that they perceived the two-coloured object as novel, and had perceived one single colour object behind a semi-transparent object during habituation. However, even if infants perceive processes such as simultaneous contrast and scission on some tasks this does not guarantee that infants are able to integrate these different processes in a way that causes them to perceive the Munker-White illusion. One

study has claimed that infants perceive the Munker-White illusion from as early as 4-months old (Yang et al., 2010). However, the current study questions the validity of this claim.

4.2.3. Examination of Yang et al. (2010)

In Yang et al.'s study, stimuli were made up of three colours (figure 4.2): red, pink, and yellow, displayed so that the yellow would be perceived as more saturated in one stimulus (on the left) than the other (on the right), despite having the same chromaticity. Infants prefer colours which are perceived as more saturated (Teller & Bronson-Castain, 2004), and so it was expected that if infants can perceive the illusion they would prefer to look at the side with the more perceptually saturated yellow. Infants did indeed look longer at this stimulus. A potential alternative explanation for this finding is that infants looked longer at that stimulus as it had a greater amount of red than the other stimulus as prior studies have found that infants look longer at red than some other colours (Franklin, Bevis, Ling, & Hurlbert, 2010, Franklin, Gibbons, Chittenden, Alvarez, & Taylor, 2012). Yang et al. attempted to control for this with a second pair of stimuli which had the same ratios of colour than the original stimuli, but where the three colours were shown spatially separately (see bottom panel of figure 4.2). Infants did not have a preference for the stimulus with more red when shown in this form. It was therefore inferred that infants' preferences reflect their ability to perceive the Munker-White illusion.
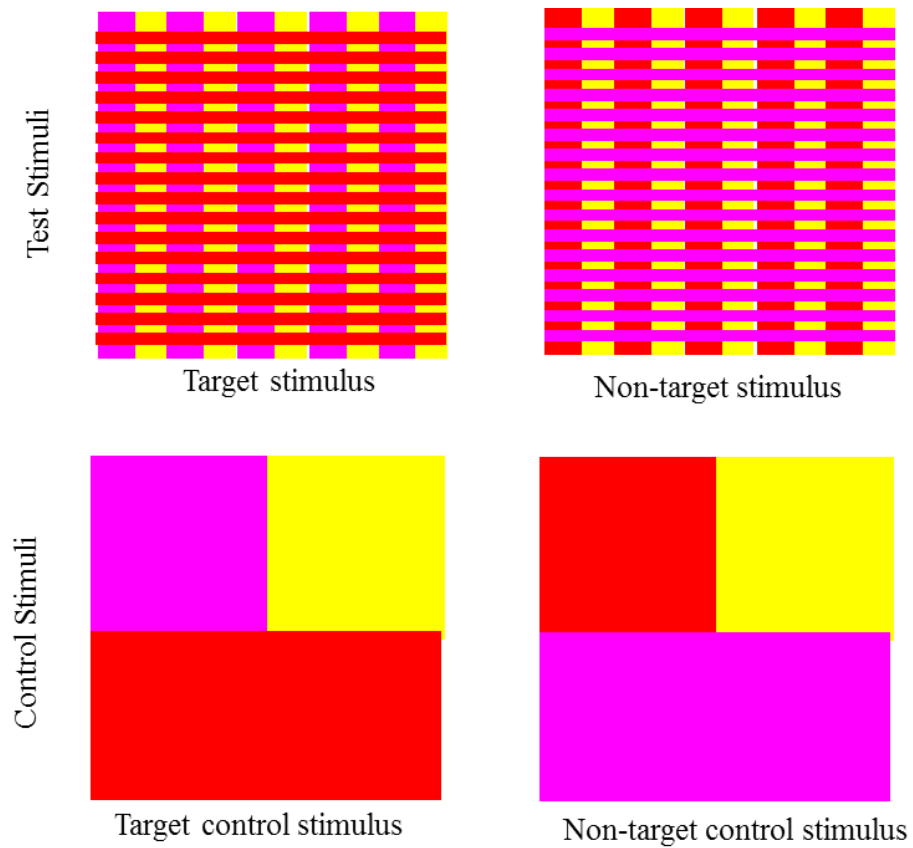
Figure 4.2. Examples of composition of the stimulus sets used in Experiment 1, stimuli here are illustrative, and not exact replicas of the actual stimuli used. Test stimuli are illusory stimuli, although the red, yellow, and pink elements of the two stimuli are identical, the yellow in the target stimulus appears more saturated than the yellow in the non-target stimulus. Control stimuli are composed of the same colours in the same ratios as the colours in the test stimuli.

Here we question the conclusions of Yang et al.'s study. Our main concern is that the perceived illusory difference in the saturation of the yellow is noticeable but small even to adults, and we question whether infants would be able to discriminate such a small difference in perceived saturation. Discrimination of

saturation increases by a factor of 1.4-2 with each doubling of age across the

lifespan (Knoblauch, Vital-Durand, & Barbur, 2001). Given that the perceived

difference in the saturation of the yellow is small for adults we question whether it

would be discriminable for infants given their much smaller saturation thresholds.

We also consider whether the control in Yang et al. does indeed rule out

alternative explanations for infants' preference. The control aims to control for a

priori preferences for red as an alternative explanation. However, there is more

varying in the illusory trials than just the amount of red. For example, the target

stimulus is perceived as 'warmer' than the non-target stimulus and whether or not

the red colour is in the foreground or background of the stimulus also differs. We

therefore propose that Yang et al.'s conclusion that infants perceive the Munker-

White illusion is unsafe – there are potential other explanations for infants

response.

4.2.4. The current study

In the current study we present two experiments which investigate

whether infants really do perceive the Munker-White illusion. First, given concern

over whether infants really could discriminate such a small perceived difference in

saturation in Yang et al.'s study, Experiment 1 presents a straightforward

replication of Yang et al's original study. One possibility is that the effect in Yang et

al. is actually a type 1 error. Replication is important in developmental science

particularly given the variation in effect sizes often found across studies as a result

of a noisy participant population (Duncan, Engel, Claessens, & Dowsett, 2014). It is

also in all research not uncommon to have varying p values across many

replications, even though there is no change in population effect (Cumming, 2011),

meaning that replications are valuable for gauging a measure of the true effect of

the experimental manipulation. Second, given concern over the stimulus design

and control in Yang et al., Experiment 2 presents a new method and stimulus set

for studying the Munker-White illusion in infants. This method controls for

potential a priori preference confounds and we choose illusory stimuli that should

be discriminable for infants. The experiment aims to enable us to more confidently

determine whether infants are responding on the basis of the physical

characteristics of the stimuli or their perceived illusory content.

4.3. Experiment 1: Replication of Yang et al

Experiment 1 is a straightforward replication of Yang et al., we also measure

infants' eye-movements with an eye-tracker to provide greater precision on infant

looking.

4.3.1. Method

4.3.1.1. Participants

Twenty five participants (11 male) aged between 4-8 months (M_{age}= 200.96

days, SD=54.13) took part in the study. A further 2 were tested but excluded due to

fussiness. In the final sample, 12 infants were aged between 4-6 months (M_{age}=

148.54 days, SD=18.76, and 13 were aged 6-8 months ((M_{age}= 249.64 days,

SD=15.35). In Yang et al (2010) there were 28 infants in total, with 14 infants in

each age group. . All infants were full term, weighed over 2500g at birth, and had

no known neurological of visual conditions, and parents reported no family history of colour deficiency.

4.3.1.2. Apparatus and set up

Infants sat in a car seat 50cm from a 22" Mitsubishi DiamondPlus 230SB Diamondtron CRT monitor, with a resolution of 1600x1200, and a refresh rate 85 Hz. Eye-movement data was recorded via SR Research Eyelink 1000 system using remote tracking.

4.3.1.3. Stimuli

There were two sets of stimuli; test and control. Both sets were replicas of those used in (Yang et al, 2010). The test stimuli consisted of 118 horizontal stripes of either red (CIE x = 0.575, y = 0.347, Y (lightness) = 24.2) or pink (CIE x = 0.306, y = 0.186, Y(lightness)=24.2). These stripes overlapped a set of vertical stripes alternating yellow (CIE x = 0.410, y = 0.487, Y (lightness) = 40.5) and either red or pink (figure 4.2). This results in the yellow appearing more saturated in one image than in the other; the perceived more saturated stimulus (with red overlapping stripes) is the 'target' and the perceived less saturated stimulus (with pink overlapping stripes) the 'non-target' (pink overlapping stripes).

In order to asses if infants will look longer at stimuli with higher proportions of red, the control stimuli were blocks of the same red, pink, and yellow in the same spatial area of colour as the test stimuli. The control stimulus with a greater amount of red is referred to as the target control stimulus (figure 4.2).

4.3.1.4. Procedure

Infants watched cartoons whilst the eye-tracking camera was set up, and then completed a 5 point calibration. Infants were centrally fixated by a black and white looming attention getter before each trial appeared, as well as between trials.

Participants were first shown two 15 second trials with the target and non-target stimulus counter-balanced for left and right location, followed by two 15 second trials with the control stimuli counter-balanced for left and right location.

4.3.2. Results

Traditional null hypothesis significance testing is accompanied throughout all experiments by Bayes factors to aid with interpretation of the data. Bayes factors allow richer interpretation of the strength of the evidence for either the null or alternative hypothesis, (Dienes, 2014). A (B) of 0.33 indicates evidence for the null hypothesis, and a ($B)$ of 3 and above indicate substantial support for the alternative hypothesis. Values close to 1 suggest that the data is not sensitive enough to concretely support either the null or alternative hypothesis (Wetzels & Wagenmakers, 2012))

As in the original study, infant looking time to the target stimulus was converted to proportional looking (looking time to target/ looking time to target + non target).The mean total looking time of the two trials for 4-5 month infants (M= 17656.31ms, SD= 6907.21ms), and for 6-8 month old infants (M=21147.15ms ,

SD=4017.67ms) was not significantly different to the mean looking times reported

for these age groups (19200ms and 19400 ms) in Yang et al (2010) (4-5 month old

infants, t (12)=-0.806, p=0.436, BF=0.361, 6-8 month old infants, t (13)= 1.253,

p=0.232, BF=0.520). If infant looking behaviour is driven by a perceived higher

saturation in the yellow, then they should look longer at the target stimulus during

the test trials. This appeared to be the case, participants looked proportionally

longer at the target stimulus than the non-target stimulus (53.89% vs 46.11%, see

the left most column in figure 4.3). However, this was not supported by analysis

via a one sample t-test against chance (0.5), t=1.738, p=0.094. A Bayes Factor

calculated with the method of Dienes (2008), with a standard deviation of 0.2

(chosen to reflect the distribution of novelty preferences usually found in infant

research), supported that there was no significant difference from chance,

BF=0.04. Analysis by age group revealed that neither 4-5 month olds or 6-8 month

old show a significant preference for the target stimulus (younger infants,

t(12)=1.338, p=0.206, BF=0.03, older infants, t(13)=1.133, p=0.278, BF=0.02).
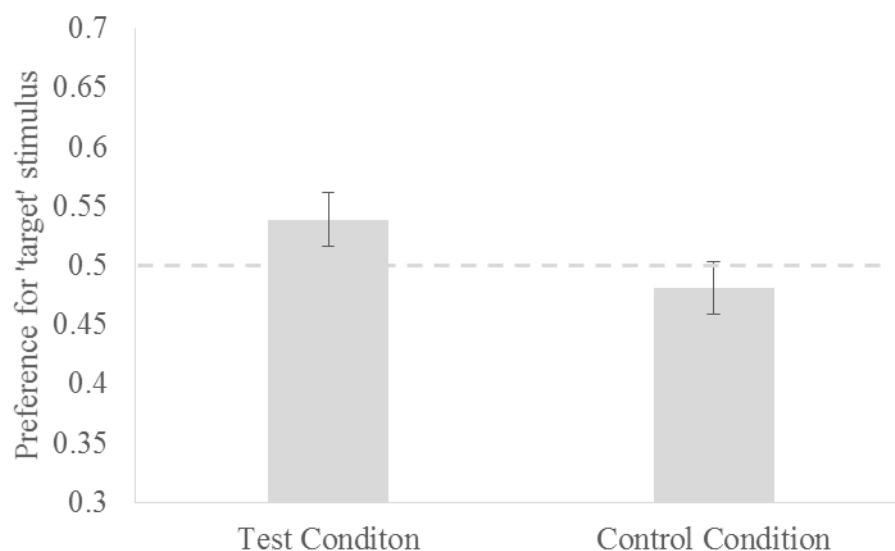
Figure 4.3. Preference for the target stimulus in the illusory (test) and control

(made up of 3 blocks of colour) conditions, where equal looking at target

and non-target stimuli would be 0.5 (dashed line). Error bars represent +/-

1SE. In the illusory condition, the target stimulus is the one where the

yellow is perceived by adults to be more saturated, and the target control

stimulus is the one with the highest proportion of red in it.

Younger infants did not look proportionally longer than older infants at the target

stimulus over the non-target stimulus on the test (illusory) trials as they had in

Yang et al. To confirm that age does not predict looking preference to the target

stimulus, we ran a linear regression with age as a predictor variable, and found no

significant relationship between looking preference and age, $F(1,27)=0.003$,

$p=0.95$, BF=0.35.

Infants did not look significantly longer at the control target stimulus than the non-

target control stimulus (52% vs 48%, see right-hand column in figure 4.3). This

was supported by one sample t-test to chance (0.5), $t(26)=-0.975$, $p=0.338$, BF=

0.01, There was no relationship between age and looking preference for the

control stimuli. A linear regression with age as a predictor on looking preference

was non-significant, $F=1.249$, $p=0.274$, B= 0.36.

4.3.3. Experiment 1 Discussion

Yang et al's hypothesis was that if infants could perceive the Munker-White illusion, they would look for longer at the target stimulus during test trials due to the increased perceived saturation of the yellow. In the current study, we do not replicate the findings of Yang et al: infants did not look significantly longer at the target illusory stimulus. Bayes factors indicate that we can have confidence in this null effect: the null result is not an issue with power and we have sufficient evidence in support of the null. The samples of infants used across studies is very similar, using the same age ranges, and approximately the same number of infants (25 vs 28 infants), and the analysis reported here is the same as that carried out in Yang et al's (2010) study.

One explanation for the lack of preferential looking at the target than non-target stimulus in the current study is that Yang et al.'s stimuli do not produce a large enough illusory effect for infants' to discriminate. As outlined above, what motivated the replication was concern over whether or not the perceived difference in the saturation of the yellow in the stimuli as a result of the illusion really is discriminable for infants. To verify this concern, we checked how similar the two yellows are perceived for adults and whether this perceived difference is above discrimination thresholds for infants. To do this we asked 3 adults to choose a yellow stimulus with a computerised colour-picker that matched the perceived yellow in both test stimuli. The difference in the perceived yellows was on average 5.84 ΔE units in a perceptual colour space (CIE LUV, 1976), whereas Knoblauch et al. (2001) report average saturation thresholds of 21 ΔE at 4-months

old. This supports our suspicion that the stimuli used by Yang et al. may well be unsuitable for assessing the Munker-White illusion in infants.

4.4. Experiment 2: A new design and stimulus set for assessing the Munker-White illusion in infancy

The lack of replication of Yang et al. in Experiment 1 re-opens the question of whether infants do perceive the Munker-White illusion. Experiment 2 aims to adopt a more appropriate stimulus set for testing the illusion in infants and a design which more effectively isolates an illusory response. The design relies on the method of habituation, and the design can distinguish whether infant looking at test is driven by the physical or illusory perceptual difference in the stimuli, where the differences are above infant detection thresholds. The method also aims to control for infants' a priori colour preferences.

Infants are first shown coloured rectangles on a red and purple striped background. These rectangles represent the physical match to the embedded rectangle used during the habituation phase, the perceptual match to this colour when viewed as part of the illusion, and a third completely novel colour. Following this, during the habituation phase infants are shown two identical stimuli where one of the rectangles of colour during the a priori preference phase is either presented on a red background with overlapping purple stripes, or a purple background with red stripes. If infants perceive the illusion then during the habituation phase they will habituate to the illusory perceived colour of the embedded rectangle, and not the physical colour of it. During the test phase infants should look longer at the perceptual match than the physical colour, as the

perceptual match is novel to them. As longer looking in the test phase of

habituation tasks can be interpreted as a familiarity preference (Houston-Price &

Nakai, 2004), a completely novel colour different to those seen in the illusory

stimulus is also presented at test in order to distinguish whether infant responding

at test is driven by novelty of familiarity. If infants look for longest at this

completely novel colour, we can infer that longer looking at either the perceptual

or the physical matches is the result of a novelty preference, and not a familiarity

preference. Finally, we also control for a priori preferences by comparing infant

response to the test stimuli pre- and post-habituation.

4.4.1. Method

4.4.1.1. Participants

Thirty four infants (17 male) aged between 4-8 months (M_{age}=190 days,

SD= 37.05) took part in the study. A further 6 infants were tested but excluded due

to a family history of colour deficiency (N=2) or not completing all test trials (N=4).

All infants were full term, weighed over 2500g at birth, and had no known

neurological or visual conditions, and parents reported no family history of colour

deficiency.

4.4.1.2. Apparatus and set up
The apparatus and set up were the same as in Experiment 1.

4.4.1.3. Stimuli

Stimuli were either patches of colour on a striped background (for pre- and post-habituation phases of the study, see procedure), or patches of colour on a coloured background overlapped by stripes (for the habituation phase).

Each stimulus is made of three colours; the two colours which make up the background/foreground stripes, and a third patch of colour. The third colour was either a *physical* match to the rectangle in the illusory trials, a *perceptual* match to the appearance of the coloured rectangle in the illusory trials, or a *novel* colour which is not close in appearance to the perceptual or physical colour patches on other trials, but of a similar lightness as the physical and perceptual match. A novel stimulus was included to aid with interpretation of the results post-habituation. To find these perceptual matches, 8 adults (Mage= 23 years) were presented each of the stimuli in the illusory pair individually, and asked to adjust a coloured rectangle (presented on a background of red and purple stripes) to match their perception of the rectangle in the illusory stimulus. Participants could adjust the colour in hue, saturation, and lightness, and stimuli were displayed in the same size as they were used in the infant experiment.

As the illusion can be seen in two ways (with red stripes overlapping the patch, or purple stripes overlapping the rectangle), there are two stimulus sets which differ in illusory and perceptual match stimuli.
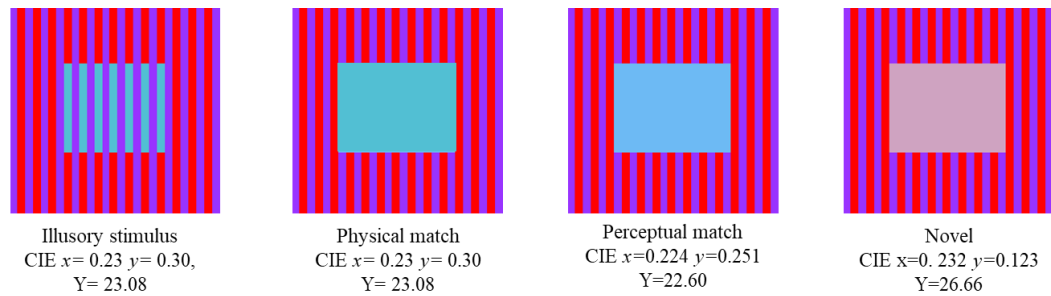
Illusory stimulus
CIE *x*= 0.23 *y*= 0.30,
Y= 23.08

Physical match
CIE *x*= 0.23 *y*= 0.30
Y= 23.08

Perceptual match
CIE *x*=0.224 *y*=0.251
Y=22.60

Novel
CIE x=0. 232 *y*=0.123
Y=26.66

Figure 4.4. a) Examples of stimulus set, i) illusory stimulus, stimulus used in habituation phase of study composed of a patch of colour on either a red (purple) background with purple (red) stripes overlapping. ii-iv) non-illusory stimuli, patches of colour on red and purple striped backgrounds, used during pre/post habituation trials; a physical match to the rectangle under the stripes in i), a perceptual match, and a novel colour. The chromaticity and luminance co-ordinates of the stimuli (in CIE colour space) are given below each stimulus. Note, due to differences in monitor displays, printing, and size of the stimuli, colours may not appear correctly in the above figure.

The Euclidean distance between the different coloured rectangles ranged between 26.08 ΔE - 93.98 ΔE in a perceptual colour space (CIELUV, 1976), which is above the average chromatic discrimination threshold at 4-months (21 ΔE) as reported in Knoblauch et al (2001).

4.4.1.4. Procedure

There were three phases to the experiment: a priori preference; habituation; and test phases. During the a priori preference phase, participants

were shown the non-illusory stimuli in pairs. All non-illusory stimuli were paired with each other, with each trial being seen twice counter-balanced for left and right location of stimuli giving a total of 6 randomly presented trials, each presented for 3 seconds. This initial phase was to assess a priori preference for the different stimuli prior to habituation and test.

During the habituation phase, infants saw 3 x 15 second trials of the illusory stimuli, where both stimuli on the left and right of the screen were identical. Participants were randomly allocated to habituation condition, seeing either the coloured rectangle on a red background with purple over lapping stripes, or a purple background with red overlapping stripes. Finally, in the test phase, participants saw the same 6 trials as during the a priori preference phase, again randomly presented for 3 seconds each.

4.4.2. Results

First, we check whether infants habituate to the illusory stimulus shown in the habituation phase. An ANOVA with Trial as a factor revealed a significant decrease in looking times across habituation trials, $F(2,66)=6.49$, *p*= .003, BF=12.56 (figure 4.5).
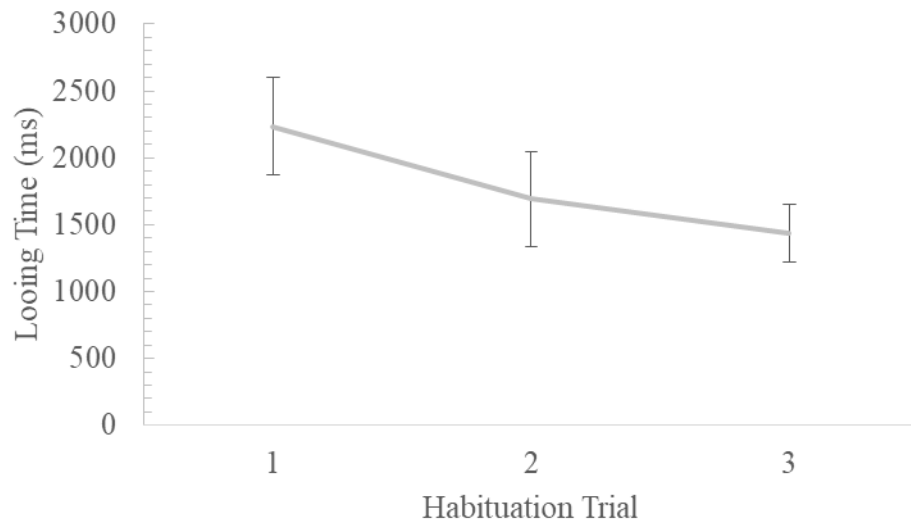
Figure 4.5. Looking time (ms) to illusory stimuli shown across three trials during

the habituation phase of the experiment. Error bars represent +/- 1SE.

Second, we assess infant looking time at test. If infants see the rectangle of colour

during the habituation trials as its physical colour, as opposed to its illusory colour,

then participants will look for longer at the perceptual match and novel stimulus

during the test trials, as these would be the least familiar to them. However, if

infants see the illusion during the habituation trials, we expect that they would

look for longest at the *physical* match, and the novel stimulus. In order to control

for a priori preferences we also compare looking time at the three stimulus types

at test post-habituation to pre-habituation.

Infant looking time to test stimuli was analysed with an ANOVA with Stimulus

Type (physical match, perceptual match, or novel colour) and Time (pre-

habituation or post-habituation), with age as a covariate (figure 4.6). There was no

main effect of Stimulus Type $F_{(2,64)}=0.556$, $p=0.576$, BF=0.131, or of Time (BF

1.147 , insensitive), crucially, there was no significant interaction between time

and stimulus type, F(2,64)=0.011, p=0.989, BF=0.202. There was no difference in

performance with age, as there was no Age*Time*Stimulus interaction
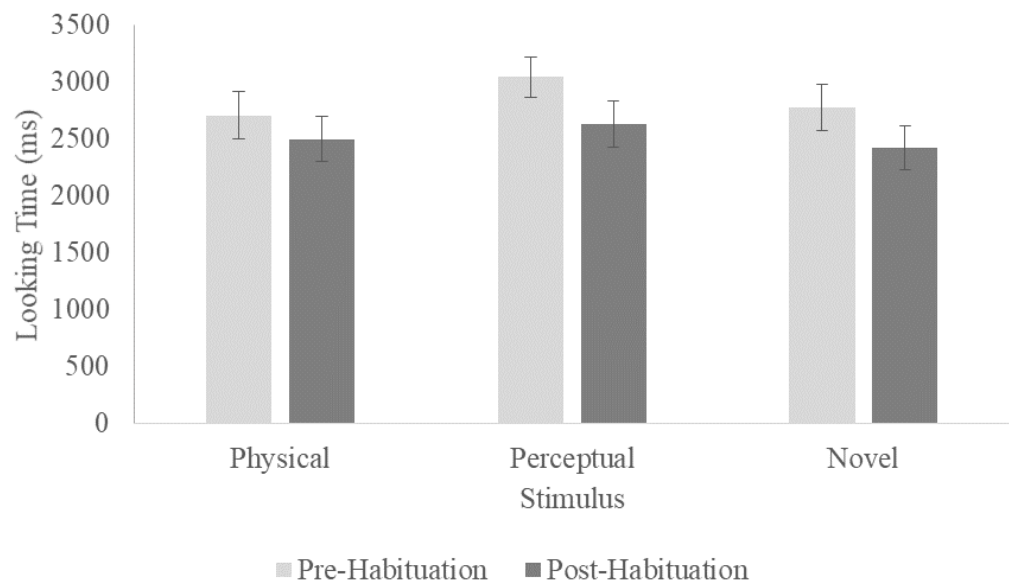
F(2,64)=0.004, p=0.996

Figure 4.6. Total looking time at each stimulus (physical match, perceptual match,

or novel) pre and post habituation. The maximum possible looking time at a

stimulus would be 12000 ms. Error bars +/- 1 SE.

4.4.3. Discussion

Experiment 2 aimed to establish whether or not infants perceive the

Munker-White illusion with a more appropriate stimulus set and design than Yang

et al.'s original study, using the method of habituation. Infants did habituate to the

illusory stimulus during the habituation phase, however, their looking time did not

differ across the 3 stimulus types at test. Infants looked equally at test at the stimulus which had a patch of colour that matched the physical colour of the illusory stimulus, and the stimulus which had a patch of colour that matched the illusory perception of the illusory stimulus, and a completely novel stimulus. Comparison of pre- and post-habituation looking times at the three stimuli also revealed that habituation to the illusory stimulus did not affect looking times to the stimuli: the pattern was the same pre- and post-habituation.

We expected that infants would show a change in preference to the perceptual and physical matches of the illusory stimuli pre- and post- habituation, and that which stimulus the infants looked at longest at test would indicate whether the colours of the illusory stimulus are perceived as illusory or not. However, the lack of looking difference to three stimulus types does not support the hypothesis that infants perceive the illusory colour but also does not support the hypothesis that they perceive the illusory stimulus as a straightforward physical representation. The sensitive Bayes factor for the lack of interaction between Stimulus Type and Time indicates that we can be confident of our null effect and that the lack of effect is not due to issues of power.

The finding of the current experiment therefore suggests that the method is not sensitive enough to reveal whether infants' respond differently to illusory or physical representations of the habituated stimulus. One possibility is that infants did not sufficiently encode the differences in the physical, illusory and novel stimuli before and after habituation. The high contrast red and purple stripes which surrounded the rectangle of colour which varied across conditions could potentially have provided too much of a distraction for infants to encode the colour

of the rectangle. In support of this explanation, at test infants only spent 15% of the time looking at the coloured rectangle and 85% looking at the red and purple stripes. This low proportion of looking time at the coloured rectangle could indicate that infants did not encode the critical part of the stimulus for the rationale of the experiment. Therefore, although we believe that Experiment 2 has many improvements relative to Yang et al.'s design (perceived stimulus differences were above infants discrimination thresholds; a priori preferences were controlled for and physical and illusory responses could be determined at test), the experiment is also unable to reveal whether infants' perceive the Munker-White illusion.

4.5. General Discussion

Here we present two experiments which aim to establish whether infants perceive the Munker-White illusion. Experiment 1 does not replicate Yang et al.'s (2010) finding that infants look longer at a stimulus that has greater perceived saturation due to the Munker-White illusion. We propose that the lack of replication is not surprising since the perceived difference in saturation between the two test stimuli as a result of the illusion is very likely below threshold for infants at the age tested. We therefore consider it likely that Yang et al.'s finding is a type 1 error. Using Bayes Factors demonstrated that there was evidence in to support the null hypothesis, and so the null finding is not a result of reduced power. Experiment 2 aimed to address some of the stimulus and design limitations of Yang et al,'s study. The experiment chose stimuli that were intended to maximise the illusory effect, where the difference between colours was above

threshold for infants. The design also enabled us to control for infants'

spontaneous colour preferences, and there were clear predictions on how infants

would respond if they saw the illusion or not. However, despite these stimulus and

design improvements, Experiment 2 was unable to decipher whether infants

perceive the Munker- White illusion as infants looked equally at 2 test stimuli that

matched the physical characteristics or the illusory perceptual characteristics of a

habituated stimulus. A further analysis of infant looking times suggested that

infants may have been distracted by the striped background of the stimuli rather

than looking at the critical coloured central rectangle and as a result differences in

looking time across stimuli were not found. Therefore, overall, we cannot answer

the question of whether infants perceive the Munker-White illusion, and the lack of

replication of Yang et al reopens this question for further investigation.

There are several options for how to take the question of whether or not infants

see the Munker-White illusion forward. One option would be to simplify the

variation across stimuli by testing the achromatic version of the Munker-White

illusion. In this version of the illusion, the perceived difference varies only in

lightness and there are no changes in hue or colour temperature. Again the size of

the perceptual effect of the illusion is quite small, and so it may be necessary to test

older infants at a point where their visual sensitivity is developed enough to detect

these small changes. Another option would be to find an alternative design that

builds on the improvements in the design in Experiment 2 but where infants will

not be distracted by the striped background at test. For example, one idea would

be to make the rectangle in the test stimuli dynamic as movement is likely to aid

with perception and attention in infants (Otsuka & Yamaguchi, 2003).

The current study illustrates two major challenges in investigating illusions in infancy. First, it should be clear what the expected responses from infants would be if they can see the illusion or cannot see the illusion. Preferential looking as used in Yang et al can represent infants' ability to discriminate between the two physically different stimuli but this does not necessarily mean that they also see the illusion. Alternative looking time paradigms such as habituation (as used in e.g. (Tsuruhara, Nakato, Otsuka, & Kanazawa, 2011) study of the hollow face illusion) provide a less ambiguous alternative, but again, only when there is are clearly expected patterns of behaviour expected from infants who can and cannot perceive the illusion. Second, a priori preferences must be measured or accounted for appropriately. Infant looking behaviour and preference for stimuli can change with context, something which control stimuli must consider. Often the relationship between parts of a stimulus such as the spatial relationship or colour ratio is changed in studies of visual illusions to 'break' the illusion to provide a control condition (e.g. Kavšek, 2009; Kanazawa,, Kitaoka, & Yamaguchi, 2013). However, this can provide a new context for the same elements of the stimuli which could influence infant looking behaviour in a different way to the test condition. To best interpret the results of a study, infants' a priori looking preferences for stimuli must be accounted for.

Although studying the development of visual illusions in infants is challenging, visual illusions are a central part of human perception and are therefore important to understand. Studying illusions across development can give us an insight into how physiological and psychological processes develop. Illusions which are the result of low-level mechanisms (e.g. Mach bands, caused by lateral-inhibition)

provide another method of tracking the development of physiological processes

across infancy. Many illusions which are not low-level are the result of an attempt

to integrate statistics about the current scene with our previous experience with

the environment (Corney & Lotto, 2007), and so may offer insight into how infants

and children learn to integrate information from their experience and their current

environment. Therefore, the endeavour of establishing what visual illusions

infants can see is a worthwhile one, and the current study identifies key issues that

should be considered in further research.

Chapter 5. Colour vision is aligned with natural scene statistics at 4 months of age

Skelton, A. E., Franklin, A., & Bosten, J.M, *for submission to Nature.*

5.1. Abstract

Visual perception in human adults is optimised to represent the statistical regularities of natural scenes (e.g. Párraga, Troscianko,& Tolhurst, 2000; Simoncelli, 2003). In infancy and early childhood, visual input is required to drive visual development (Blakemore, & Cooper, 1970; Berardi, Pizzorusso, & Maffei, 2000; Knudsen, 2004), but we do not know if higher order scene statistics are extracted and represented. In adults, sensitivity to different hues shows an asymmetry, which relates to the statistical regularity of colour in the natural world. We measured infant colour discrimination to investigate whether or not the visual system in very early life can represent higher order scene statistics. Our results reveal that even as young as four months of age, colour vision is aligned with the distribution of colour in natural scenes. This is the earliest association between vision and natural scene statistics that has been found. Our measurement and analysis of full psychometric functions for infants and adults has additionally revealed that independent processes govern visual performance at different chromatic intensities. This additional finding suggests that the different choices of threshold criteria that are typically applied in the field of psychophysics may lead to different conclusions about the underlying visual processes.

5.2. Main

Human perception is optimised in many ways to extract information from the environments that we find ourselves in. These calibrative processes occur over different time scales, both over evolutionary history (Hansen, Throsten, & Gegenfurtner, 2009), and within the lifetime of the individual (e.g. Wachtler, Doi, Lee, & Sejnowski, 2007). Some calibrative processes undoubtedly occur in infancy: for example, face (e.g. Kelly et al 2007), speech (e.g. Kuhl et al., 2006) and music (Hannon & Trehub, 2006) perception "narrow" during infancy to show biases for the stimuli encountered in infants' individual environments. In mature perceptual systems, there is tuning to higher-order statistical regularities of visual scenes, thus visual channels are optimised to extract the regularities of spatial frequency (Hansen & Hess, 2006; Knill, Field, & Kersten, 1990; Tadmor & Tolhurst, 1994), orientation (Hansen & Essock, 2004), and attributes of colour (Long, Yang, & Purves, 2006) in natural scenes. Relatively little is known about when during visual development representations of the statistical regularities of natural scenes arise. Ellemberg et al. (2012) have found that representations of the spatial frequency structure of natural scenes was present in 10 year-olds but undeveloped in 6- and 8- year-olds. The only existing work on infants has shown that 9-month olds prefer a violation of natural texture representations only under some conditions (Balas & Woods, 2014) – conclusions about the alignment between infant perception and natural scenes cannot be securely drawn.

Colour vision is a good example of a perceptual system that is optimised at several levels to extract information from natural scenes. Human colour vision relies of information from three classes of retinal receptors, long- (L), medium- (M) and

short- (S) wavelength sensitive cones. The particular sensitivities of the human cones have evolved to optimally represent colour information relevant to the diets or skin colours of our primate ancestors (Changizi, Zhang, & Shimojo, 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 reduce information redundancy about natural scenes (Ruderman, Cronin, & Chiao, 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 & Gegenfurtner, 1992; Pearce et al., 2014; Álvaro, Linhares, Moreira, Lillo, & Nascimento, 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 5.1a). It is the blue-yellow axis that contains most variance in natural scenes (Webster & Mollon, 1997; Bosten, Beer, & MacLeod, 2015), see figure 5.1b & c for an example of the variation found in natural scenes).

Figure 5.1. a) The MacLeod Boynton chromaticity diagram representing the chromatically opponent channels of colour vision (L/(L+M) and S/(L+M)), the location of the blue-yellow axis is approximately along the negative

diagonal of this figure. b) an example of a natural scene, and c) a histogram

showing the density and distribution of chromaticities of the natural scene

(b) in the MacLeod Boynton chromaticity diagram. The largest variance in

chromaticities can be seen to fall along the negative diagonal.

In the present study we investigated the time course of development of

representation of the statistical distribution of colours in natural scenes by

measuring colour discrimination in infants. We chose infants aged 4-6 months

because existing data show that the S-cone reliant colour subsystem develops

relatively late at 2-3 months (Bornstein, 1975; Brown & Teller, 1989; 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 5.2).
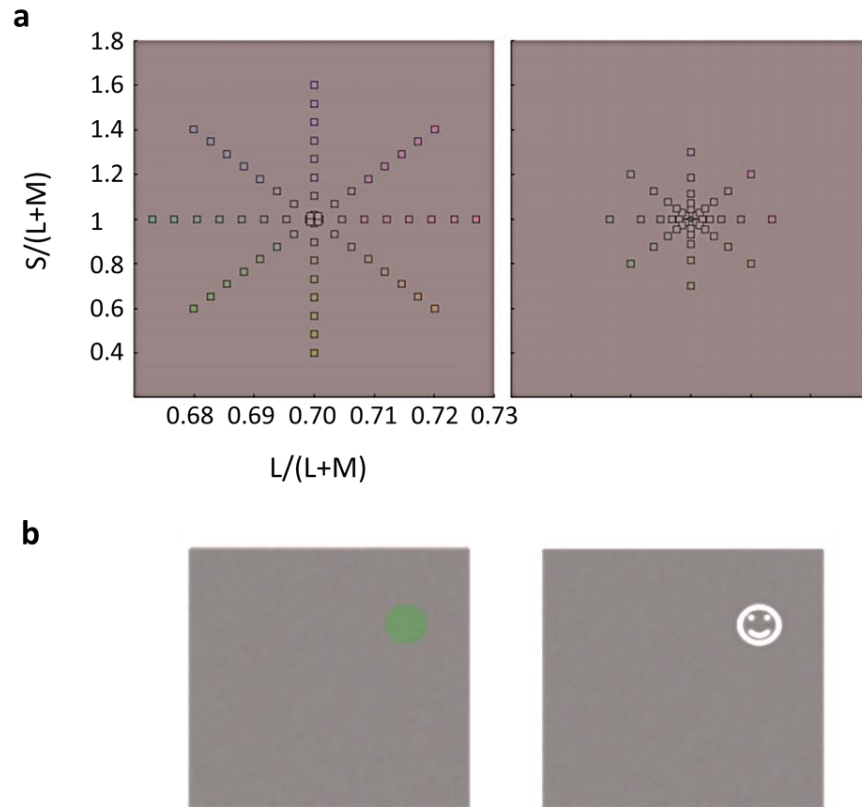
Figure 5.2. a) Infant (left) and adult (right) target chromaticities along the 8 individual axes presented in a version of the MacLeod Boynton chromaticity diagram. Towards the centre of the figure, colours are less saturated, increasing in saturation radially along the axes. b) Example target (left) is displayed within 6.9⁰ of the participants' fixation point. If the target is fixated for a minimum of 160ms, the target is replaced by a smiley face (right), and a noise is played, and is recorded as a 'hit' for this trial. See appendix B, figure 9.2 for full example of trial progression.

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) along the resulting psychometric function (Figure 5.3a). 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 the MacLeod-Boynton chromaticity diagram (MacLeod & Boynton, 1979). We

chose the MacLeod-Boynton diagram as a colour metric because it represents

along its cardinal axes activity in the two predominant 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. Any bias in colour discrimination, such as a blue-yellow bias, means that

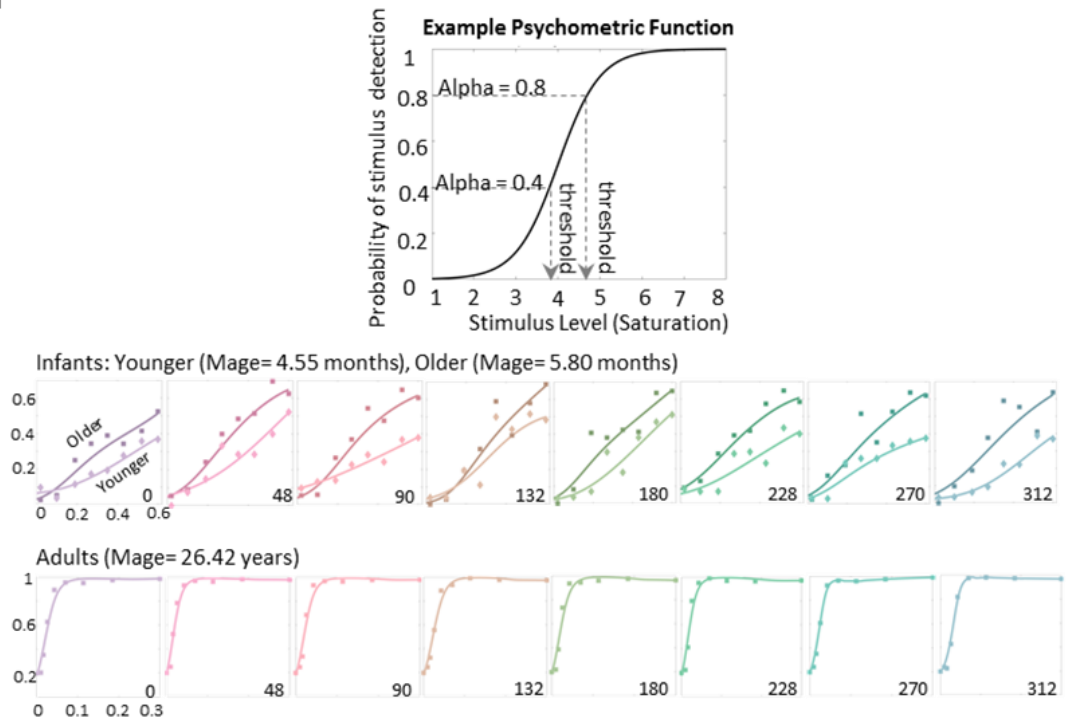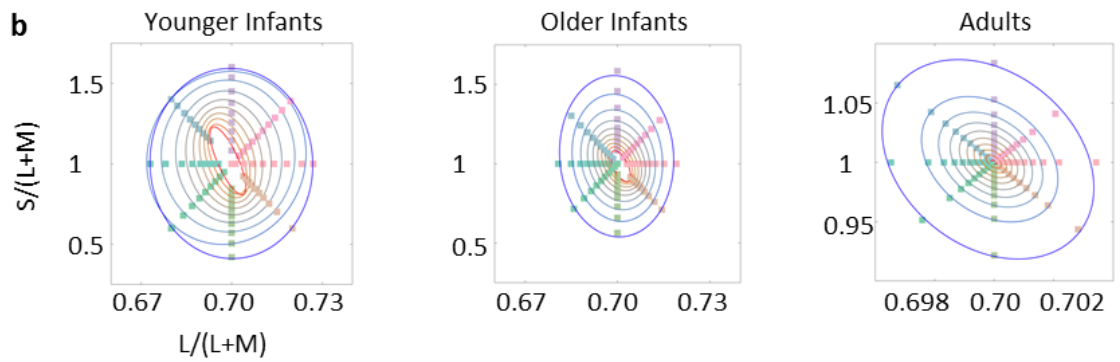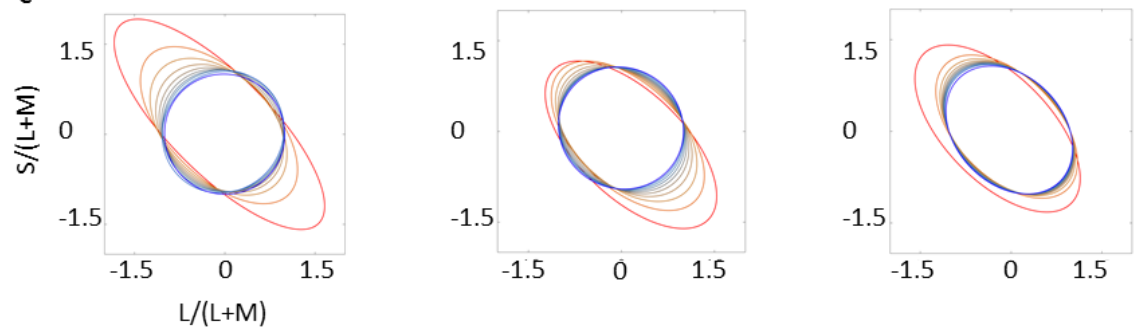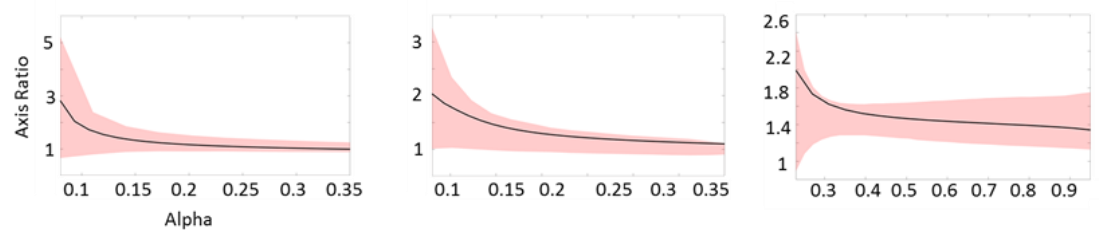discrimination must be determined by non-cardinal colour mechanisms.

a

Example Psychometric Function

Infants: Younger (Mage= 4.55 months), Older (Mage= 5.80 months)

Adults (Mage= 26.42 years)

b

Younger Infants   Older Infants   Adults

c

d

Figure 5.3. a) Example psychometric function, and psychometric functions for

infants and adults across the 8 axes of the MacLeod Boynton chromaticity

diagram, all showing probability of target detection as a function of

stimulus intensity (saturation). The example psychometric function

demonstrates how different alpha criterion result in different threshold

measurements along the same psychometric function. For the infant and

adult data, each individual graph shows psychometric functions for a

specific axis in the MacLeod Boynton chromaticity diagram, noted by angle

in the bottom left of each figure. Thresholds were extracted at a range of

alphas, and then used to fit ellipses to the three sample groups; two infant

groups (younger and older than the infant sample median age) and adults.

b) Resulting discrimination ellipses across a range of alpha criterion for

younger, older, and adult participants in the MacLeod Boynton chromaticity

diagram. Axis ratios are calculated from ellipses (c) plotted in a normalised

version of the MacLeod Boynton chromaticity diagram. In both 5.3b and

5.3c, ellipses fitted from thresholds extracted at lower alphas are redder in

colour, and those from higher alphas are bluer in colour. d) Axis ratios as a

function of alpha with bootstrapped 95% confidence intervals.

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 quantify 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 in the colours of natural scenes.

We were able to achieve very clear group psychometric functions for each of the

three age groups and for each hue (Figure 5.3a). One obvious difference between

the groups is in the position of asymptotes. For adults, performance quickly

asymptotes close to 100%. For younger infants the asymptotes is at about 30-40%

and for older infants 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 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. Figure 5.3b 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 a blue-yellow colour direction, as would be expected if colour

vision is aligned with the statistics of natural scenes. Figure 5.3c shows axis ratio

as a function of threshold alpha. For infants, axis ratios are large at low alphas

(2.82 for younger infants at alpha=8%, 2.04 for older infants at alpha=8%), 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. The

figures show bootstrapped 95% confidence intervals for each group: for older

infants at the lower alphas the confidence intervals do not include 1, indicating

that population mean shows worse discrimination along the blue-yellow axis than

along the orthogonal axis. 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 Appendix B). Here, we found that there is a significant effect of alpha on axis

ratio for both infants (Skillings-Mack, T(19)=274.64, p=<.001) and adults ($\chi2(19) =$

31.47, $p =. 025$).

We propose that the strong dependence of axis ratio on alpha that we observe for

infants is because visual factors limit performance at the lower reaches of the

infant psychometric function. At low alphas, where there is the greatest degree of

uncertainty in perceptual decision-making, infants are relying on tiny visual

signals to generate an above-chance performance. However, at high alphas the size

of the visual signal is sufficient for detection, but performance is still significantly

below 100%. We propose that at these high alphas other factors such as attention,

motivation and gaze control are what limits performance. This account fits well

with the idea that colour discrimination is tuned to scene statistics: where visual

processes are most important in determining colour thresholds, the chromatic bias

in detection performance is most aligned with the distribution of colours in natural

scenes.

Our results show that like adults, infants show a bias in colour discrimination in a

direction predicted from the distributions of colours in natural scenes, maybe as

early as 4 months of age. Even though there is a significant increase in colour

discrimination performance with age (see Appendix B, 8.4), the discrimination

ellipses show no evidence for development in the degree of bias (figure 5.3b). Our

results are compatible with two schemes: either bias in colour discrimination is innate, perhaps calibrated to natural scene statistics neurogenetically, or that 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 colour discrimination bias 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 commonly applied. For example, in a 4-alternative forced-choice task the 81% point is often selected as the threshold criterion (Watson and Pelli, 1983) Our finding implies that the choice of alpha may have a significant impact on the conclusions of psychophysical studies, and that actually a lower alpha than is typically chosen may better isolate the sensory processes that psychophysicists are interested in.

The relationship between axis ratio and alpha that we have observed would not have been apparent if we had not measured full psychometric functions. Typically in infant studies, discrimination performance is measured using the 'preferential looking' technique, where gaze duration in the presence and absence of a stimulus is compared statistically. This typically 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 are broadly comparable with our own, but owing to the time consuming nature of the method, are available for only a limited number of colour axes (see Appendix B, 8.5). Our method of measuring detection performance using eye movements (see

also Jones, Braddick, Atkinson, & Nardini, 2015) 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 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 which has only demonstrated statistical optimisation of perception 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. Our additional psychophysical finding that different processes predominate at different regions of the psychometric function has implications for interpreting prior and future psychophysical data on a broad range of perceptual processes.

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7. Appendix A- Supplementary information for Paper 1.

7.1. Discrimination and novelty preference

The definition of categorization is that 'discriminable stimuli are treated equivalently' (p. 52, Quinn, 2003). One possibility is that a lack of a novelty preference could indicate that infants cannot actually see the difference between colours rather than indicate that infants can discriminate the colours but treat them equivalent in memory. We predicted, on the basis of a study of infant chromatic thresholds (Knoblauch et al, 2001), that all chromatic differences should be discriminable for infants since all chromatic differences were larger than the average chromatic discrimination threshold at 4-months (threshold estimated to be 21ΔE units in CIELAB colour space (Knoblauch et al, 2001): the smallest difference in the current study was 28ΔE and the average was 62.38 ΔE for the smaller pairs and 109.47 for the larger pairs. However, there are difficulties in inferring discriminability from other studies which used different stimuli (e.g., Knoblauch's estimates were for chromatic differences from neutral along protan, deutan and tritan axes, and the threshold estimates also had a good deal of variability). In addition, even if all chromatic differences were above chromatic thresholds, it is possible that those stimuli with novelty preferences are more perceptually dissimilar. Therefore, in order to further understand the relationship between discrimination, perceptual similarity and novelty preference we take two approaches. First, we investigated the relationship between infants' novelty preferences and the similarity of colours by testing whether the size of colour differences in a perceptual colour space and adult similarity ratings of the colours

predicted infants' novelty preferences. Second, we made additional measurements

which directly tested infant discrimination of four of the colour pairs (two with

novelty preferences and two without) to check that colours which failed to elicit a

novelty preference could be discriminated in other contexts, and to assess the

relationship between discriminability and novelty preference.

7.1.1. Measurements of discrimination and perceptual similarity for stimulus pairs

We tested discrimination and perceptual similarity using a target detection

task developed by Franklin, Pilling and Davies (2005). In our target detection task

a coloured target is seen on a coloured background and eye-movements are

recorded with an eye-tracker to measure how well infants can discriminate the

target from the background. Low-pass luminance noise was added so that the

target could only be detected on the basis of the chromatic difference of target and

background and not on the basis of luminance (colours were isoluminant for the

average adult observer which is a good estimate of infant isoluminance

(Pereverzeva, Hui-Lin Chen, Plamer, & Teller, 2002). The task was also made to be

gaze-contingent such that a visual and auditory reward was played when the

target was fixated and the next trial commenced automatically following target

fixation (as in Jones et al, 2013). Four stimulus pairs were tested from green-

yellow and purple-red regions. For both regions, two adjacent pairs were sampled,

one pair with a novelty preference and one without. We check whether these pairs,

which include two of the smallest chromatic differences (in CIELAB), can be

discriminated in the context of the target detection task, and compare the

perceptual similarity of the colour pairs.

Of course, if infants can discriminate the colours in the context of the target

detection task it does not necessarily indicate that they can be discriminated when

seen in the context of the novelty preference task as the spatial characteristics of

the task differ. As the stimulus pairs in the target detection are abutting as figure

and ground, this could lower discrimination thresholds on the task relative to the

test phase of the novelty preference task where the two different stimuli were

surrounded by a neutral ground. Unfortunately, in infants it is not possible to

measure discrimination of two stimuli using looking measures when the stimuli

are shown side by side on a neutral ground as in the novelty preference task but

without a familiarization phase. Infants may look longer at one stimulus than the

other which would indicate discrimination, but may not have a looking preference

and still be able to discriminate them (e.g., be able to discriminate blue and red but

look at them equally). However, the target detection task does provide a measure

of relative perceptual similarity across the colour pairs. If novelty preferences are

based on how different colours look rather than their categorical relationship, then

the pairs for which there were novelty preferences should have greater target

fixation than the pairs with no novelty preference.

7.1.2. Methods

7.1.2.1. Participants.

Twelve 4-6 month old infants took part, with 2 infants excluded due to

infant fussiness.   The final sample (8 males) had a mean age of 22.63 weeks (SD

2.65). All infants had a birth weight greater than 2500g and no known visual or

neurological conditions.

7.1.2.2. Apparatus and Stimuli.

There were four stimulus pairs, sampled from the main experiment from green-yellow (2.5Y-10Y; 10Y-7.5GY) and blue-purple regions (2.5 P-10P; 10P-7.5RP). The luminance and chromaticity co-ordinates (CIE x,y,Y, 1931) of the Munsell stimuli and the grey background for the novelty preference task were measured with a photospectrometer (spectrascan PR6500) in the viewing booth and under the same lighting conditions as the novelty preference task. These x,y,Y were then rendered on a calibrated 22-in. Mitsubishi DiamondPlus 2070SB Diamondtron CRT monitor with a resolution of 1600 x 3 x 1200 pixels, 24-bit colour resolution, and a refresh rate of 100 Hz. Stimuli were displayed via a PC driven Cambridge Research Systems ViSaGe MKII Stimulus Generator. Stimuli were shown as a coloured circular target (which subtended a visual angle of 6.9°), on a coloured background which filled the entire screen, with low pass luminance noise (12 cd/m^2). The experiment took place in a blacked-out booth with the monitor being the only source of light. Eye-movements were recorded with an Eyelink 1000 eye-tracker (SR-Research), placed immediately in front and below the monitor, and the central point of the monitor screen was at the participants' eye-level at a distance of 35 cm. Participants were sat in a car seat that was fixed to a stable chair.

7.1.2.3. Design and Procedure.

Infants were shown a cartoon whilst the eye-tracker was focused on their eye, and this was followed by a four-point calibration. On each trial, the coloured target was displayed simultaneously with the coloured background up until target fixation but not longer than 2250 ms. Fixation was defined as 160ms of continuous looking at one point, as in Jones et al (2014). If the target was fixated, the program automatically displayed a smiley schematic face in the same location as the target (of the same size, with eyes and mouth defined in gray) and a simple melody was played for 500ms. Following this, or after 2250 ms if there was no target fixation, the next target and background were presented, with the target location constrained with the target positioned at a random location 6.9° of visual angle from the infants' initial point of fixation (Jones et al, 2014). If infant gaze strayed from the screen, the trial was discounted, a looming and contracting black and white attention getter was displayed centrally and the next trial was onset once the attention getter was fixated. In addition to the four stimulus pairs from the novelty preference task, and a condition where the target and background were the same colour (7.5 B) in order to estimate chance performance on the task. The allocation of each colour in a stimulus pair as target or background was counterbalanced, and trial order was randomized. Trials continued until infant looking at the screen waned or until a maximum of 120 trials had been completed.

7.1.3. Results and Discussion

The percentage of trials where the target was fixated was calculated for the

four green-yellow and purple-red stimulus pairs (hit rate), and the condition

where target and background were identical (guess rate). Figure 7.1 gives the

guess rate and the hit rates for the four pairs (left side of the figure) with the

novelty preferences for the same pairs from the main experiment for comparison
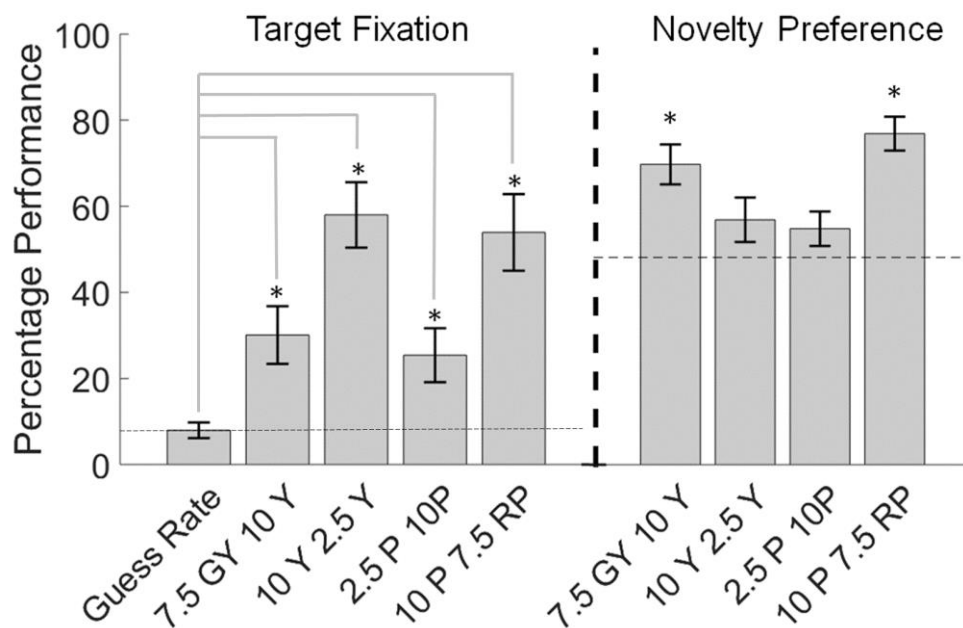
(right side of the figure).

Figure 7.1. The average percentage of targets fixated (left side of figure) for the

four pairs tested in the target detection task, with novelty preferences from

the main experiment for comparison (right side of figure). The dashed line

in each panel indicates chance performance (also indicated by the guess

rate in the target fixation panel). Asterix indicate pairs for which the

evidence was in favor of H1 when compared to chance.

Bayesian paired samples t-tests (with a Cauchy prior of 0.707) revealed that for all

four pairs the target was fixated at a rate greater than chance, meaning that all four

colour pairs were discriminable: 7.5GY-10Y, $t(9)=3.13$, $p=.01$, $B=5.32$; 10Y-2.5Y,

$t(9)=2.77$, $p=.02$, $B=3.31$; 2.5P-10P, $t(9)=8.04$, $p<.001$, $B=1081.83$; 10P-7.5RP,

$t(9)=6.11$, $p<.001$, $B=175.26$. Moreover, fixation was not more likely for the two

pairs which elicited novelty preferences (7.5GY-10Y & 10P-7.5RP, mean=42.18,

SD=18.41) than the two pairs which did not (10Y-2.5Y & 2.5P-10P, mean=41.98,

SD=5.85), $t(9)=.09$, $p=.93$, $B=.31$. These findings clearly show that colour

differences which failed to elicit a novelty preference are discriminable by infants

in other contexts. Even if the context of the target detection task enhances

discriminability, novelty preferences are unlikely to be simply related to

perceptual similarity since targets for colour pairs with greater novelty preference

were not always fixated at a greater rate than colour pairs with no novelty

preference.

In sum, we show here that infants' novelty preferences are unlikely to be due to

discriminability or perceptual similarity as: i) all colour differences were above

estimated average chromatic thresholds; ii) novelty preferences do not relate to

chromatic differences in perceptual colour space, and iii) chromatic differences

which failed to elicit a novelty preference are discriminable in other contexts and

not always detected more readily than chromatic differences with a novelty

preference. We therefore suggest that infants' pattern of novelty preference

indicates that infant colour memory is governed by the categorical relationship of the colours.

The current study demonstrates that colour categories affect infant hue memory. Another question is whether colour categories themselves affect perception (categorical perception, Franklin, Pilling, & Davies, 2005). That question is different to the one addressed in the target detection experiment outlined above. The experiment above seeks to obtain a measure of perceptual similarity to see whether perceptual similarity rather than categories can account for infants' novelty preferences. An experiment that tested categorical perception would need to instead equate same- and different-category chromatic differences in discrimination and see whether categories affect perceptual similarity. Franklin et al. found that coloured target detection was faster when on different- than same-category coloured backgrounds, when the chromatic differences were equated in CIE perceptual colour space (Franklin, Pilling, & Davies, 2005). However, as discussed above, it is an assumption that adult and infant perceptual colour spaces are similar, and equating stimuli in discrimination rather than perceptual similarity would be more logical for testing categorical perception. One approach which may clarify whether colour categories affect infant perceptual similarity would be to equate same- and different-category colour differences in the number of just-noticeable differences and then test whether the categorical status affects target detection when chromatic differences are suprathreshold. This approach was adopted by (He, Witzel, Forder, Clifford, & Franklin, 2014) to investigate the time course of colour category effects in adults, and when colours were equated in just noticeable differences (JNDs), colour categories affected post-perceptual

processing around 200 ms from stimulus onset. Now that the current investigation

has identified infants' categorical distinctions, the approach taken by He et al. can

be applied to infants.

7.2. A priori preference

Infants have a priori preferences for looking longer at some hues (e.g., reds

and blues) than others (e.g., yellow-greens) (e.g., Franklin et al, 2008; Franklin,

Bevis, Ling, & Hurlbert, 2010; Zemach & Teller, 2007; Brown & Lindsey, 2013). The

current study controlled for such a priori preferences by counterbalancing across

infants which stimulus was novel for each pair of stimuli. Due to this

counterbalancing, preference for a certain hue (e.g., blue) is unlikely to account for

novelty preference for a stimulus pair (e.g., blue and green) as half of the infants

saw a given hue as the novel colour and half as the familiar hue – when novelty

preference is averaged across infants the effect of any a priori preferences should

cancel out (Franklin, 2009). Mean novelty preferences were in fact highly similar

irrespective of which stimulus in each pair was novel and which was familiar: the

discrepancy in novelty preference was on average only 5%. In addition, a priori

preferences are unlikely to account for novelty preferences as a priori hue

preference in infants varies smoothly with hue and therefore two similar hues are

unlikely to elicit a large difference in looking times (Brown & Lindsey, 2013). An

analysis was conducted to confirm that a priori preferences could not account for

variation in novelty preference across stimulus pairs. The average looking time at

each hue during the familiarization phase was used as an index of a priori

preference. Looking time during the familiarization phase is a valid index of a

priori preference as prior research has established that infants' a priori

preferences for hues are comparable whether hues are presented singly (as in the familiarization phase) or as pairs (as in the test phase) (Bornstein, 1975). The average familiarization looking time at a stimulus (during either the first trial or across all familiarization trials) did not predict infants' novelty preference for that stimulus, largest R^2 = .004, smallest p=.38, largest B=.14. Likewise, the difference in average familiarization looking time for the two stimuli in each pair did not predict the variation in novelty preference across pairs, R^2 = .009, smallest p=.19, largest B=.22.

7.3. Familiarization and novelty preference

Figure 7.2 provides the average looking time at hue during the 8 familiarization trials and the novelty preference scores for pairs of adjacently sampled hues (adjacent pairs) and larger hue pairs which straddle pairs where no novelty preference was found (large pairs). A repeated measures ANOVA with hue (14 levels) and trial (8 levels) as factors revealed a linear trend for trial, $F(7,1148)$= 53.965, p=<.001, B=3.29E+74, on infant looking time during the familiarization phase. There was no interaction of trial and hue, $F(14,164)$ 1.28, p=.225, B=.002).
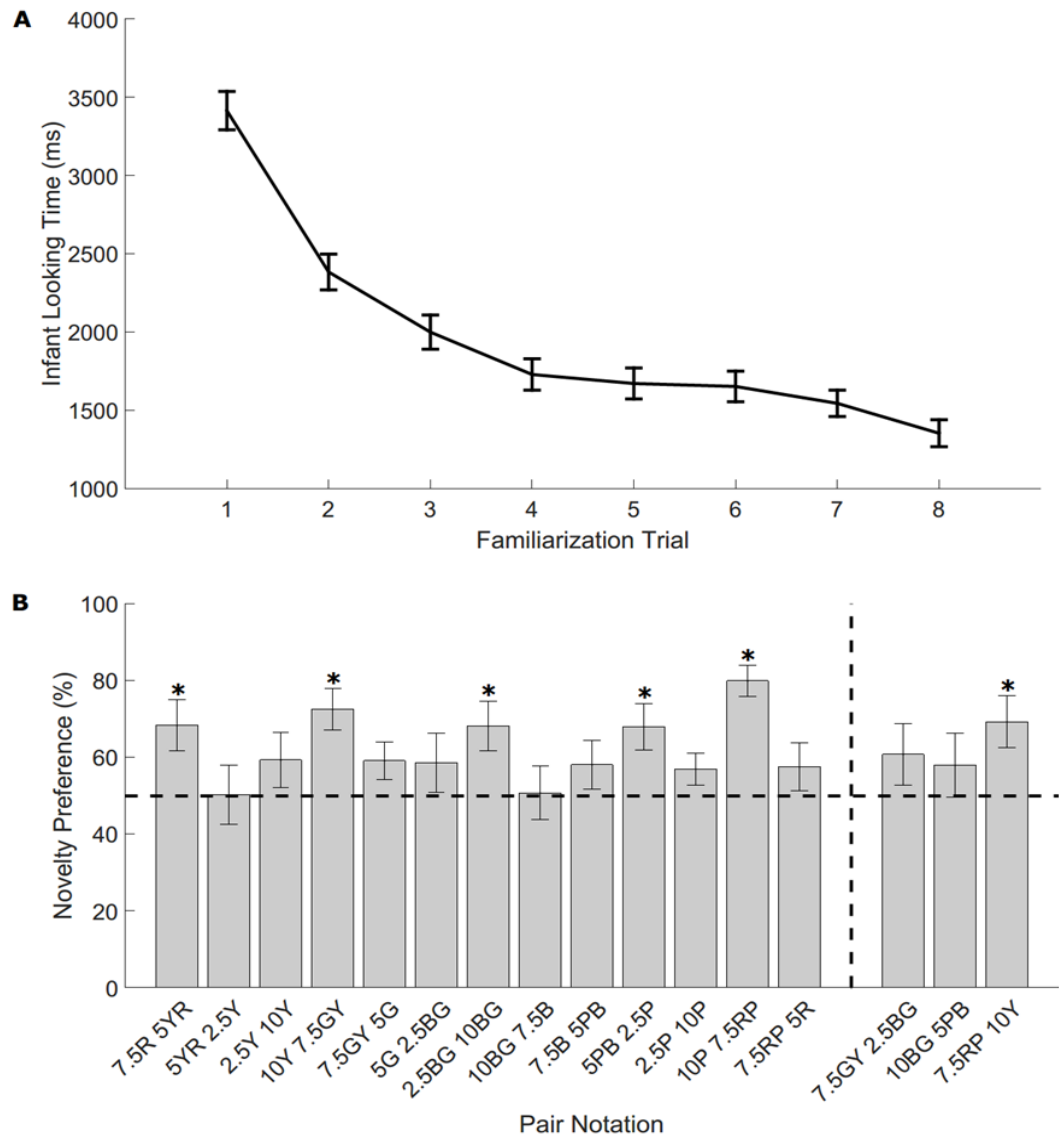
Figure 7.2. (A) Infant looking time during the familiarization trials averaged across hues (+/-1se). (B) Novelty preference percentages (+/-1se) for pairs of adjacently sampled hues (pairs on left of vertical dashed line in figure) and larger hue pairs which straddle smaller pairs (pairs on right of vertical dashed line in figure). Asterisk indicate novelty preferences which produce a Bayes factor in Support of H1 relative to H0 (B>3), with equal looking at novel and familiar hues indicated by the dashed line at 50%. Munsell codes of hues of each pair are given.

7.4. Analysis of WCS centroids

To investigate the hypothesis that infant colour categories are organized

around hues that are commonly central to lexical categories, we conducted an

analysis using the WCS naming centroids (the number of times that the hue is at

the center of a WCS lexical category when plotted in a perceptual colour space

(CIELAB)). If infant colour categories do capture the common centers of lexical

categories revealed by the WCS, then the hue pairs which are categorically

different for infants (indicated by pairs with novelty preference) should span hues

which are infrequently at the centers of lexical categories (i.e. coincide

infrequently with category centroids when counted across WCS languages). We

investigated whether the combination of 5 pairs for which we find novelty

preference optimally avoids category centroids (centroid frequencies were taken

from ref 8). We consider the 13 adjacent stimuli pairs from row G, hue columns:

(3,6), (6,9), (9,12), (12,15), (15,18), (18,21), (21,24), (24,27), (27,30), (30,33),

(33,36), (36,39), (39,2). The 5 pairs corresponding to infant novelty preferences

are: (3,6), (12,15), (21,24), (30,33), (36-39).

A simple means to quantitatively assess how well the infant preferences align with

the WCS naming centroids is to assign a score to this particular configuration: the

total number of centroids between the 5 stimuli pairs (excluding the stimuli

column centroid counts). In this case, the score would be the sum of the centroid

frequencies for hue columns (4,5), (13,14), (22,23), (31,32), (37,38). We can then

examine how well this particular configuration of 5 hue pairs (corresponding to

the infant novelty preferences) ranks against any of the 1287 possible combinations of 5 hue pairs, by computing the score of each of these configurations. To do so, we first computed the naming centroids over all 110 languages in the WCS, following Kay and Regier (2003). We then explicitly computed the score for all 1287 possible combinations of 5 hue pairs, using the centroid counts along the stimulus row that we sampled from (row G). We found that only 4.27% of the 5 pair combinations (55/1287) resulted in a lower total centroid count than the 5 pairs which infants had novelty preferences for (i.e., more optimally captured hues that are not central to lexical categories).

Additionally, we used the peak centroid counts for each hue at any lightness level so that the centroid peaks seen in figure 7.3 are captured in the analysis. We found that only 3.26% (42/1287) of the combinations resulted in a lower total centroid count than the 5 pairs which infants had novelty preferences for. For this peak centroid analysis, the best 5 pair combination that had the lowest centroid count included 4 of the 5 pairs for which infants showed a novelty preference, and only the blue-green pair differed (the best combination included the pair adjacent to and bluer than the blue-green pair for which infants showed a novelty preference).
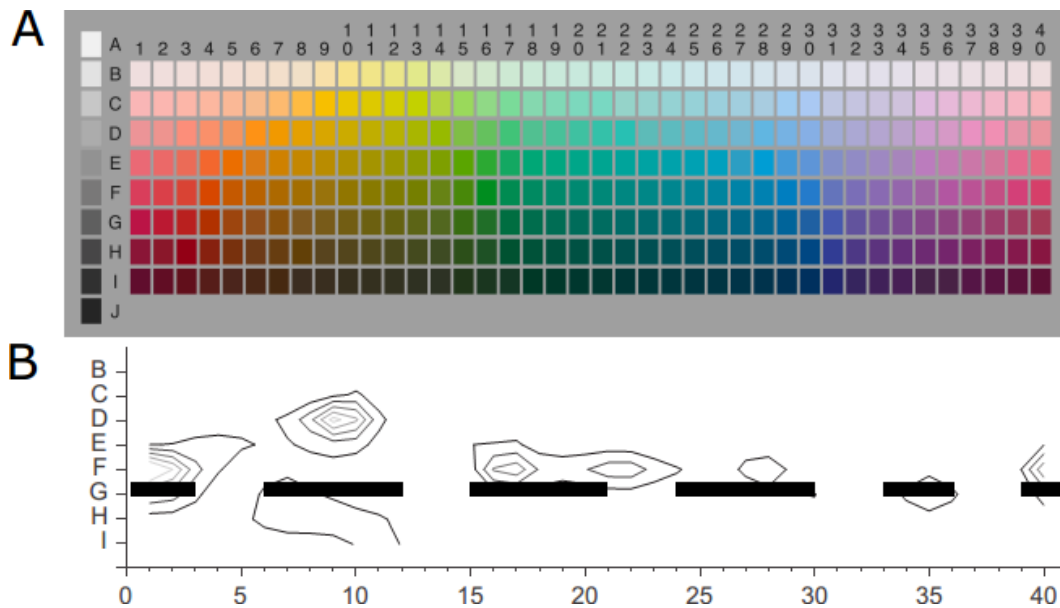
Figure 7.3. The full WCS stimulus grid and centroid analysis. A. WCS stimulus grid for 40 hues at 8 lightness levels. Stimuli in the current experiment were sampled from row G. B. Centroid analysis from Kay & Regier, 2003. The black and grey contour lines indicate the number of speaker centroids falling at that point in the stimulus grid from WCS data, with the outermost contour representing 100 centroids and each subsequent inner contour representing an increment in 100 centroids. Infant novelty preferences are indicated by the gaps in the thick black horizontal line at row G.

7.5. Stimulus positions in a perceptually uniform colour space

A series of regressions found that differences in CIE hue, CIE chroma and Euclidean difference in CIELAB perceptual colour space (figure 8.4) as predictors of novelty preference did not predict novelty preference (largest R^2=.072, smallest p=.31, B=3.28E-10). In addition, a sample of 40 adults (5 males, mean age = 21.17 years (SD=1.37) rated the similarity of hue pairs twice using a line rating scale, and

adult similarity ratings did not predict infants' novelty preference (R^2=.083, p=.28, B=1.13-09).
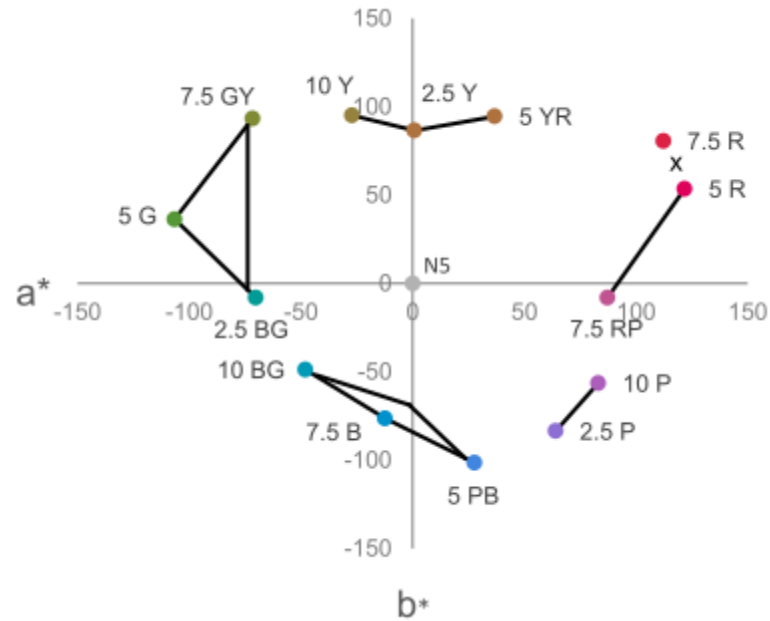

Figure 7.4. Stimuli plotted in CIELAB perceptual colour space. Stimulus pairs for

which there was no novelty preference are indicated with black lines

joining the stimuli, and pairs where there was a novelty preference are

indicated by the absence of these lines. The cross between 7.5R and 5R

indicates a pair that was not tested. Euclidean distances in this space do not

predict infants' novelty preference.

This analysis indicates that the colour pairs which infants do not distinguish in

recognition memory are not the smaller chromatic differences in adult perceptual

colour space which adults find more dissimilar than other pairs. However, one

possibility is that infant perceptual colour space at 4-6 months is different to that

of adults (even in adults CIELAB is not perfectly uniform for large chromatic

differences (Wyszecki & Stiles, 2000). A difference in infant and adult perceptual colour space would need to be radical to be able to account for the pattern of novelty preferences in our data since there was even no novelty preference for pairs with very large CIELAB differences. However, a radical difference between infants and adults is perhaps unexpected since infants are known to be trichromatic by at least 3-months (e.g., Knoblauch et al, 2001) mean adult isoluminance is a good approximation of infant isoluminance (Pereverzeva, Hui-Lin Chien, Palmer & Teller, 2002) and based on chromatic thresholds on protan, deutan and tritan axes their perceptual colour space could be predicted to be similar to that of adults albeit with poorer sensitivity (Knoblauch et al, 2001).

8. Appendix B - Supplementary information for Paper 4.

8.1. Method and analysis

8.1.1. 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 calibration phase of the study. All participants were born at 37 +/-2 weeks, met a minimum birth weight of 2500g, had no known visual deficits, and no history of epilepsy.

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) and the Lanthony tritan album, and all had normal or corrected vision.

8.1.2. 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, MacLeod & Johnson). In order to prevent individual participants detecting the target via a residual luminance difference, low-pass luminance noise was added over the whole display. The mean luminance

of both target and background was 28 cdm-2, and luminance noise was linearly distributed to range between ±10% of the mean. The chromaticities of the target stimuli varied in saturation along 8 axes within a version the MacLeod-Boynton (1979) chromaticity diagram based on the Stockman MacLeod and Johnson (1993) cone fundamentals. 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), 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 (Figure 8.1). Due to infants' lower discriminability thresholds (Knoblauch et al, 2001) stimuli were sampled from a wider range of chromaticities than adults.
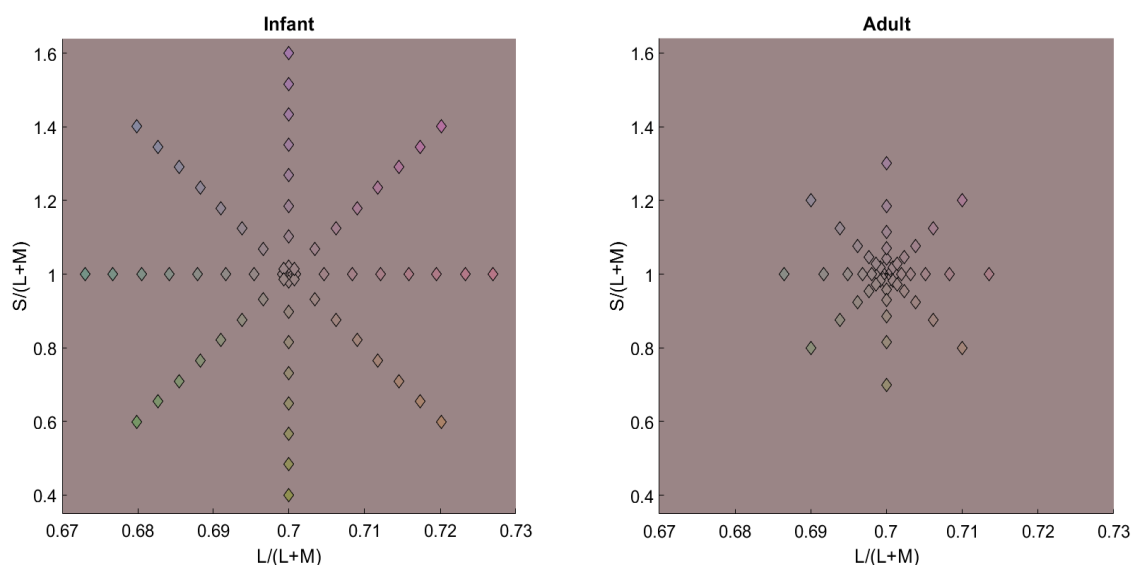
Figure 8.1. Infant (left) and adult (right) target chromaticities along the 8

   individual axes presented in a version of the MacLeod Boynton chromaticity

   diagram. Towards the centre of the figure, colours are less saturated,

   increasing in saturation radially along the axes.

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 a SR

Research Eyelink 1000 system, and the experimental programme was run in

MATLAB (R2016a, The MathWorks Inc., Nantucket, 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., Chattsworth, CA).

8.1.3. 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 participants moved a

lot), participant eye-movements were recalibrated during testing.

Before each trial, participants were presented with a blank screen of luminance

noise (duration), 250ms. Targets appeared within 6.9^o of the participants' current

fixation point to 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'), and 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 2250 ms, no auditory or visual reward

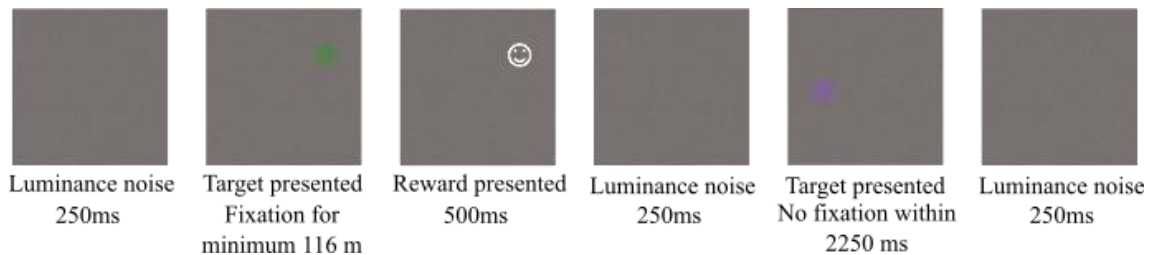was played, and a miss was recorded (see figure 9.2).

| Luminance noise 250ms | Target presented Fixation for minimum 116 m | Reward presented 500ms | Luminance noise 250ms | Target presented No fixation within 2250 ms | Luminance noise 250ms |

Figure 8.2. Example trial procedure. Participants are presented with a blank screen

of luminance noise for 250ms before a target is presented. If fixated for a

minimum of 160ms, the target is replaced by a smiley face, and a noise is

played, and is recorded as a 'hit' for this trial. After another blank display of

luminance noise, the next target is displayed and is not fixated within

2250ms, no reward is played, and the next trial starts.

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), 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.

8.2. Data and analysis

8.2.1. Infant Data

For analysis at group level, infants were split by median age into two groups (younger and older). Details of the total number of trails completed by each infant group and mean proportion of 'seen' targets are given below.

Table 1. The mean proportion of targets seen ('hits') across all trials by all infants, younger, and older infants.

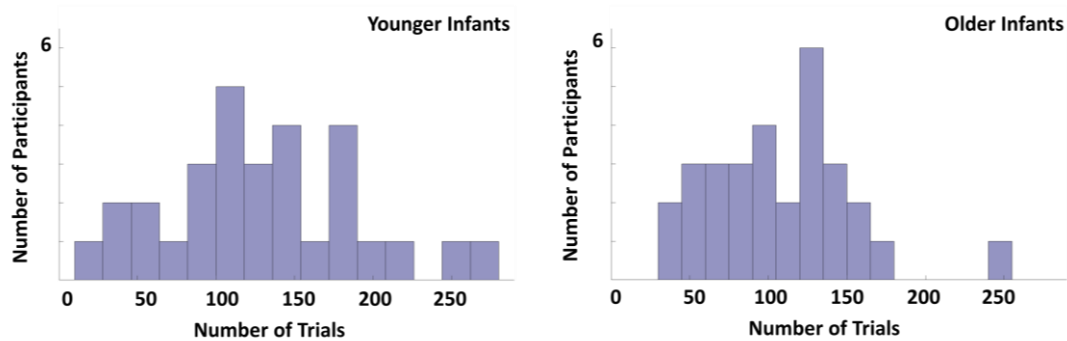| Group	Mean age months (SD)	Mean proportion of 'hit' trials (SD)
All infants	5.18 (0.76)	0.24 (0.15)
Younger infants	4.55 (0.27)	0.20 (0.13)
Older infants	5.82 (0.51)	0.29 (0.15)

Figure 8.3. Histograms of the total number of trials completed by all infants

younger infants (left, N=30), and older infants (right, N=30).

8.2.2. Infant and adult data fitting

Psychometric functions were fitted using a local linear fit (Żychaluk, &

Foster, 2009), and were best fit using a logit fit for infants, and a Weibull fit for

adult data. Lapse rate was included as a free parameter.

The guess rate parameters were estimated from empirical data on similar tasks.

Infant guess rates were taken from data from 13 infants of a similar age range to

the current study who participated in a target detection task in Skelton et al.

(2017). In that version of the task, chromatic targets were presented on a

chromatic background, including a proportion of trials which presented a target on

a background of equal chromaticity. The infant guess rate in the current study is

taken from the number of targets fixated and recorded as a 'hit' on this version of

the task: 13 targets seen from 170 targets presented, around 8%.

Adult guess rate was estimated from adults (n=5) who completed a version of the target detection task described in 9.1. The targets in this control task were from a limited sample drawn randomly from the stimuli set used in paper 4, with the addition of targets with the same chromaticity as the background. Guess rates for adults are estimated from the number of trials fixated on trials where chromaticity and background are the same: 136 targets seen of 690 presented, around 20%.

8.3. Individual participant analysis

8.3.1. Individual infant analysis

In order to fit individual infant ellipses for participants, data from the two hue angles which make up the blue-yellow axis (132° and 312°) were collapsed together, and a psychometric function was fitted. The same was also done for the two hue angles in positive diagonal (48° and 228°). As a result there were a greater number of data points for each saturation along the positive and negative diagonals than when fitting to individual hue angles, improving the ability to fit psychometric functions for each infants' data.

Three infants were excluded from this analysis as despite collapsing along the axes, they did not have enough points to fit an appropriate psychometric function to their data. As with the group level analysis, different axis ratios were extracted from different alpha criterion (see figure 9.4. for an example of the psychometric functions and axis ratio variation with alpha of a single infant participant). It was not always possible to fit an appropriate ellipse for each infant at each alpha criterion, and axis ratios which were particularly large (above 10) or small (below

0.1) were excluded from analysis. As a result, the number of participants with individual ellipses fitted within an alpha criterion ranged from 30 to 51 (see table 9.2. for details of the sample size at each alpha level).
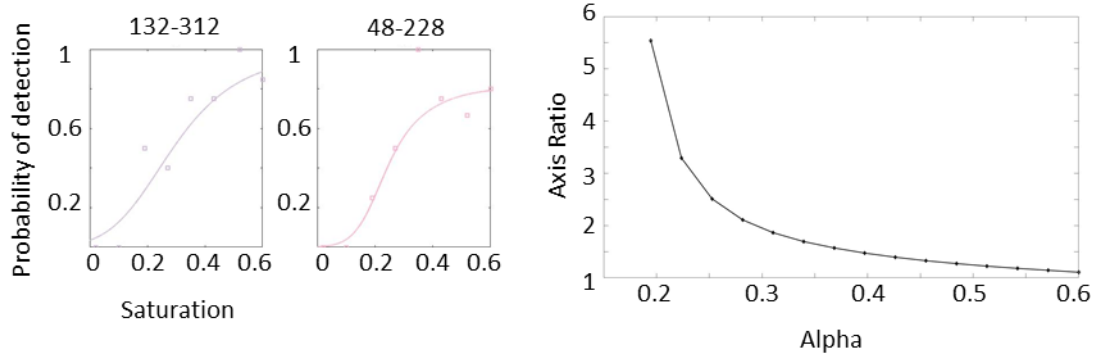

Figure 8.4. Example of an individual infants psychometric functions along the negative (48-228) and positive (132-312) diagonals diagonals of the MacLeod Boynton chromaticity diagram, and the resulting axis ratios as a function of alpha.

When axis ratios are extracted from individual infants, there was a main effect of alpha on axis ratio (figure 8.4.), with lower alphas resulting in larger axis ratios (Skillings-Mack, T(19)=274.64, *p*=<.001). Wilcoxon signed rank tests with a bonferroni correction, showed axis ratios were significantly different to 1 between alpha levels of 0.19 and 0.22 (table 8.2.)
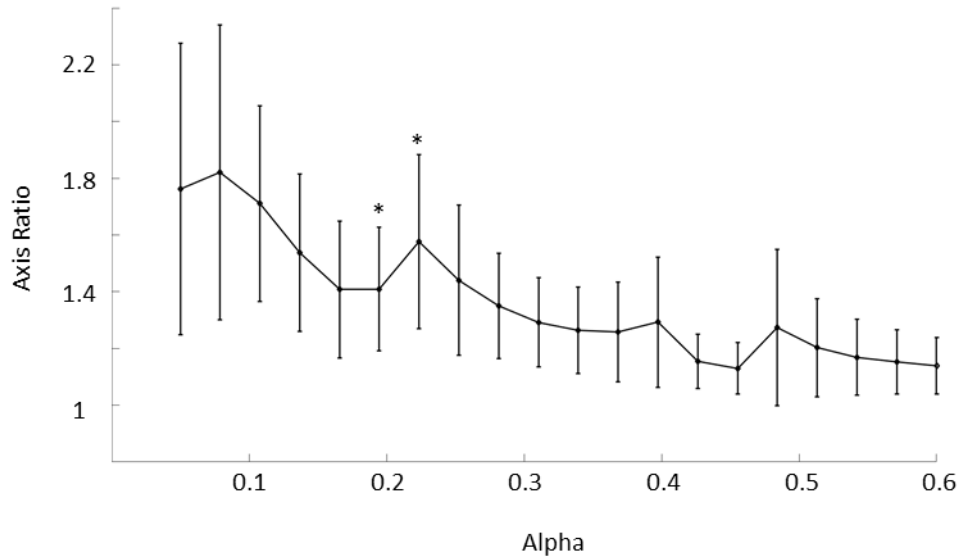
Figure 8.5. Axis ratios from 57 infants across varying alphas. Error bars +/- 1

standard error. Asterisk indicates that axis ratios are significantly different

to 1. For significance and sample size details, see table 9.2.

Table 8.2. Results of the Wilcoxon Signed Rank one sample test against 1 for infant

individual ellipses across alphas. Corrected for multiple comparisons, the critical

value for *p* is .0025, asterisks indicate values which meet this criterion.

Alpha criterion (2 d.p.)	Final n of sample	Z	*p*
0.05	30	2.09	.037
0.08	37	2.59	.010
0.11	45	2.91	.004
0.14	48	2.82	.005
0.17	50	2.82	.005
0.19	51	2.82	.002 *
0.22	53	3.05	.002 *

0.25	53	3.14	.003
0.28	52	2.96	.003
0.31	52	3.01	.005
0.34	51	2.81	.009
0.37	51	2.63	.012
0.40	51	2.51	.013
0.43	50	2.50	.028
0.46	50	2.20	.063
0.48	51	1.86	.060
0.51	51	1.88	.058
0.51	51	1.90	.076
0.57	51	1.76	.072
0.60	51	1.80	.093

8.3.2. Individual adult analysis

Due to the large number of trials adults completed (N=640) individual ellipses for adults could fitted in the same way as was done for the adult group analysis. Psychometric functions were fitted along each of the 8 axes, and saturation thresholds were extracted across varying alphas before fitting the ellipse in a normalised version of the MacLeod Boynton chromaticity diagram.

There was a main effect of alpha on axis ratios (Friedmans' anova, $\chi 2(19) = 31.47$, $p =. 025$). Wilcoxon signed-rank tests comparing the axis ratios to 1 with a Bonferroni correction applied, resulting in a significance level set at $p= .0026$. Axis

ratios were significantly different to 1 at all alpha levels (Wilcoxon signed ranks, largest *p*= .001, Z=3.3).
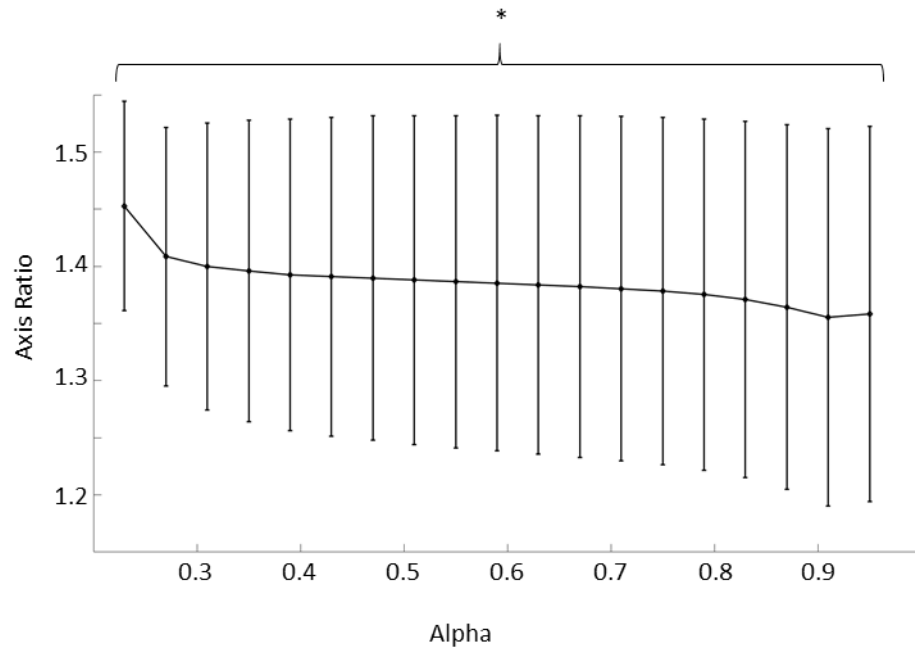

Figure 8.6. Means of individual axis ratios for adult participants at varying alpha criterion. Error bars +/- 1 SE. Axis ratios were significantly different to 1 at all alphas, as indicated by the asterisk.

8.4. Developmental progression of saturation thresholds

Another approach to assessing the development of the blue-yellow bias is to examine the developmental progression of saturation thresholds across the major axes of the MacLeod Boynton colour space. If development of the saturation thresholds of saturation thresholds along the blue-yellow axis is, for example, slower than the remaining axes, then this may suggest a gradual 'tuning' of the blue-yellow bias.

To investigate the developmental progression of saturation thresholds, data was collapsed across individual axes one the four major axes of the MacLeod Boynton chromaticity diagram; the two Cartesian axes (vertical and horizontal, 0°-180°, and 90°-270°), and the two intermediary axes (the blue-yellow axis and its reflection: 132°-312°, and 48°-228°). Thresholds were extracted from psychometric functions fitted using a local linear fit as described above (Żychaluk, & Foster, 2009). As with the main analysis, thresholds were extracted at different alpha levels. The thresholds across development were calculated with a moving age bracket which captured infant response across 5 time points across the age range of our sample of participants.

Lower saturation thresholds are found across all ages at lower alpha levels than at higher alpha levels (figure 9.7.). Infant discrimination thresholds may be underestimated in psychophysical methods which use a single criterion. The youngest infants' thresholds plateau around an alpha of 35% as this is very close to the top of the psychometric function for these participants (see figure 5.3. in the main text for comparison of asymptotes of older and younger infants). This highlights that in interpreting the developmental progression of saturation thresholds across infancy, the co-development of attentional factors which can influence infant behaviour should also be considered.
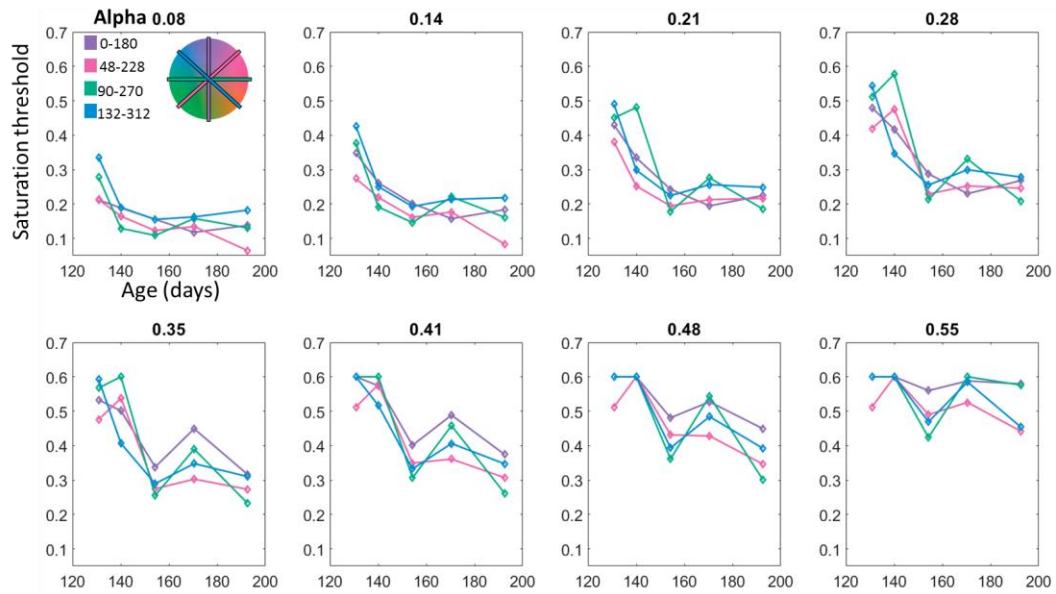
Figure 8.7. Developmental progression of saturation thresholds along 4 major axes in the MacLeod Boynton chromaticity diagram. See key in top left graph for details of the angles the major axes included, and a description of their location within the MacLeod Boynton chromaticity diagram. Each graph represents thresholds taken at a specific alpha, identified above each graph.

Across all alpha levels, thresholds decrease across all four major axes. Qualitatively this rate of improvement in discrimination thresholds appears to be roughly equivalent across the four axes. Critically for the discussion of whether alignment to natural scene statistics progresses in early infancy, there does not appear to be evidence for a particular development of bias in thresholds along the blue-yellow axis across age.

8.5. Comparison to Knoblauch et al (2001)

Previous studies have also measured chromatic discrimination thresholds in early development. Comparing discrimination thresholds recorded across studies can improve the accuracy of estimation of infant detection thresholds. Here we compare thresholds from the current study with those from Knoblauch et al (2001).

There are significant differences between the current study and that of Knoblauch et al. Firstly, the two studies are very different in design. Knoblauch et al used a staircase procedure in a forced choice preferential looking paradigm where an experimenter blind to location judged if an infant was looking preferentially to the left or right of a screen. Secondly, Knoblauch et al measured thresholds along a smaller number of axes (along three colour directions; protan, deutan, and tritan). These differences do limit the extent to which it is possible to directly compare thresholds from the two studies, however, it does provide an insight into the variability found across methods in measuring infant thresholds. Figure 9.8. compares Knoblauch et al.'s data with the discrimination ellipses measured in our study at two alpha levels, (the smallest and largest extracted).
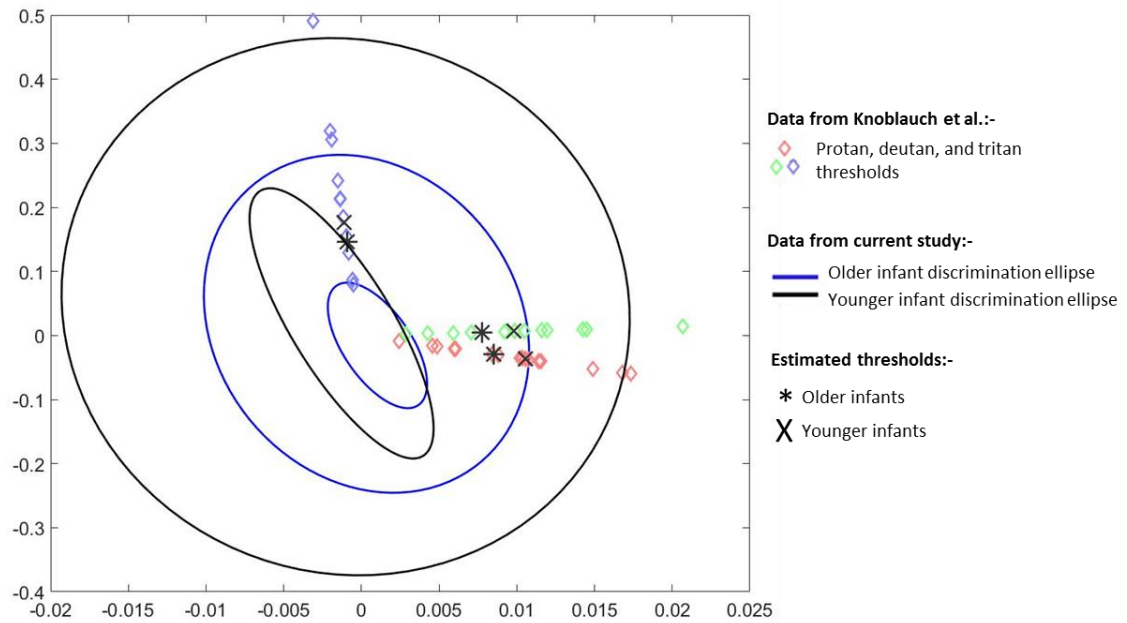
Figure 8.8. Comparison of discrimination ellipses for older (blue ellipses) and

younger (black ellipses) infants at two alpha levels (one small, one large;

0.08 and 0.55) to threshold data from individual infant participants in

Knoblauch et al (2001) along the protan (red), deutan (green), and tritan

(blue) axes of colour vision. Blue ellipses show older infant group data, and

black ellipses younger infant group data. Black cross and asterisk indicate

the estimated thresholds of mean infants in the current study based on

thresholds reported in Knoblauch et al.

The largest discrimination ellipses fitted to the infants in our sample capture the

majority of the highest thresholds measured in Knoblauch et al for infants aged

below 6.8 months (the age of the oldest infant in our sample). This suggests that

the two methods produce broadly compatible results. Often in studies if infant

chromatic thresholds few directions are tested due to the nature of testing infant

participants. One advantage of the target detection method presented in paper 4 is

that a wider range of directions in colour space can be tested with relative ease, with both individual and group level performance being possible, providing a potentially richer understanding of early perception. A second advantage of the target detection task presented here is that both infants and adults complete the same task. Often when measuring discrimination thresholds, infants and adults tasks will be different (e.g. infants' thresholds may be measured by preferential looking, whilst adults complete a 4AFC task). There is still, of course, a difference between adult and infant completion of the target detection task in paper 4 (adults having a greater understanding of what the task *is* for example, and can maintain attention for longer than infants). However, the target detection task does allow for a more in depth analysis including at varying alpha levels as opposed to having a single number as an output. This means we are able to consider the development of other limiting factors of infant performance as well as sensitivity when comparing across ages. The ability to do this shapes our understanding of the limiting factors on perception of colour across early development through to adulthood, and the relationship between the two.