Woodhead publishing series in textiles



Colour design Theories and applications

Edited by Janet Best





Understanding colour perception and preference

A. HURLBERT and Y. LING, Newcastle University, UK

Abstract: Colour is a critical cue for many vital behavioural tasks: material identification, object recognition and social–sexual signalling. Given the importance of the behavioural uses of colour, and the known perceptual and physiological properties of colour vision, it is likely that preference for coloured objects drives preference for colours themselves. The underlying universality in patterns of human colour preference (liking for blue, dislike for yellow and yellow–green) supports the notion of evolved emotional responses to colour. More recent studies demonstrate both universality and individuality of colour preference, as well as mutability across culture and age. These variations in preference, and other evidence, argue that the ability to form emotional associations to colour, whether on an ontogenetic or evolutionary timescale, is deeply embedded in human nature.

Key words: colour preference, colour perception, evolution, behaviour.

5.1 Introduction

At this point in a book devoted to theories and applications of colour perception and design, it may seem belated to ask: 'what is the use of colour?' Yet this is the question that drives many vision scientists in their attempts to understand how the human visual system works. Asking what purpose colour serves in the most fundamental behavioural tasks humans carry out, such as finding food or mates, leads us to an understanding of why colour vision evolved in the way it did, and this in turn enables us to understand how colour vision might be exploited in more complex and advanced behavioural tasks, such as choosing wallpaper for a dining room. The question is challenging because, on the most basic level, it is not obvious what purpose colour vision serves: the human visual system does not need colour to see motion, contour, or depth and therefore it can navigate the world and interact with objects without colour vision. We watch old black-andwhite movies without struggling to recognise objects, decipher emotional expressions or interpret actions; the world does not seem diminished or flat, simply monochrome. The lack of colour does not seem to impair basic comprehension of the world. So-called 'colour-blind' individuals who have poor discrimination ability in certain regions of the spectrum or who lack an entire dimension of colour vision are generally not noticeably handicapped, and historic restrictions on their employment in certain jobs (e.g. the police) are increasingly being relaxed.

Yet colour vision must have conferred a survival advantage in order to have been selected and maintained by evolution; the eye and brain devote significant processing power to seeing in colour (Gegenfurtner and Kiper, 2003); many human endeavours, from manufacturing to marketing, both scientific and artistic, make prolific use of colour; and there is a prevalent feeling that colour generally enriches and enlivens. The word 'feeling' here is deliberate and important: colour is commonly linked to feelings; people talk of strong likes and dislikes for certain colours; colours in the environment are held to influence mood and wellbeing (Kwallek *et al.*, 2007); and although the lack of colour in monochrome movies does not impair object recognition, it dramatically alters the 'atmosphere'. Why should colour have evolved to be so strongly linked with affective responses? Here we will consider the behavioural advantages conferred by colour vision which may have helped to drive its evolution, and how these may be connected with emotional responses to colour.

5.2 The origins and uses of colour vision

5.2.1 Evolution of colour vision

Humans and other Old World monkeys and apes differ from most other mammals in having three functionally distinct types of photoreceptor in the retina instead of two: the L, M and S cone types, sensitive to the long, middle and short wavelength ranges of the visible spectrum, respectively. These three cone types record the relative amounts of light in each of the three spectral bands, and the resulting triplet of responses specifies the spectrum. If two different spectra produce the same triplet of responses, then as far as the eye can tell, the two spectra are the same. Nonetheless, because there are millions of possible distinct response triplets, the eye (and brain) can distinguish millions of different colours. Thus, baboons, macaque monkeys, gorillas and humans are amongst the relatively few mammalian species who perceive a three-dimensional colour world and are able to discriminate over one million colours. Chickens, with four distinct cone types, and some stomatopod crustaceans, with 12, are even more richly endowed, but dogs, New World monkeys (living in South and Central America), mice and other mammals have only two-dimensional colour vision and are therefore theoretically limited to discrimination of only roughly 10 000 colours (Neitz et al., 2001).

The trichromatic visual system of the Old World primate species is thought to have evolved from the primitive dichromatic system of their New World cousins, after the split in the phylogenetic tree. The primitive system consists of two cone types, short-wavelength-sensitive ('S') and longwavelength-sensitive ('L') cones, with spectral sensitivities peaking around 430 nm and 562 nm, respectively (Bowmaker, 1998). Trichromatic primates possess an additional middle-wavelength-sensitive cone type ('M'), with spectral sensitivity peaking around 535 nm, thought to have derived originally from mutation of the primitive L cone-pigment-encoding (Nathans, 1999). The dichromatic system is, in turn, thought to have evolved via mutation from a single photopigment more than 800 million years ago, making it highly plausible that colour vision is 'as old as vision itself' and therefore, perhaps, as vital as vision itself (Neitz *et al.*, 2001). The divergence of the M from the L cone type is thought to have occurred approximately 30 million years ago (Jacobs, 1993). The newness of this divergence is reflected in the subtlety of the difference between the photopigments: on average, the L and M cone types differ by only about 15 amino acids, sufficient to shift the peak sensitivity by about 30 nm (Nathans, 1999).

Because of the extremely high homology (roughly 98 %) in their genetic coding, the L and M cone spectral sensitivities are highly overlapping, and therefore their responses to light tend to be highly similar. The advantage conferred by having two similarly responding receptors can be exploited only by eliminating the redundancy and maximising the differences in their responses - in other words, by decorrelating their responses. This decorrelation is carried out in the second stage of colour encoding – after the initial encoding by cone responses – by cone-opponent channels: the 'modern' L-M channel, in which the L cone signal is compared with the 'new' M cone signal, and the 'ancient' S channel, in which the S cone signal is compared with the combined L and M cone signals (Mollon, 1989). These two chromatic channels are colloquially called the 'red'-'green' and 'blue'-'yellow' channels, and form the basis for the fundamental perceptual opponency that we perceive between the hues of these names. (It must be noted, though, that the physiological cone-opponent axes are not perfectly aligned with the axes joining the perceptually unique hues of red and green, and blue and yellow, and the overall process by which first- and second-stage encoding leads ultimately to colour categorisation is far from transparent (Hurlbert 1997; Wuerger et al., 2005).)

5.2.2 Colour perception

Colour opponency is nonetheless a cornerstone of colour perception, acknowledged even before Hering (1878) sought to explain phenomena such as the occurrence of coloured after-images or the mutual exclusiveness of red and green in any one colour. Hering (1878) argued that colour vision was founded on four unique sensations corresponding to the four unique hues, and postulated the existence of physiological mechanisms which pitted red against green, blue against yellow and black against white. We now understand better the biochemical and physiological mechanisms of

chromatic adaptation – both of the retinal cones and of colour-encoding neurons at later stages of visual processing (Lennie and Movshon, 2005; Tailby *et al.*, 2008) – which contribute to coloured afterimages as well as to the fundamental phenomenon of colour constancy. Adaptation of the cones to the prevailing light levels occurs continuously as they adjust their operating range to fit their environment: as the average stimulation of the L cones increases, for example when exposed to deep sunset, the average sensitivity of the L cones will decrease, thereby maintaining their middle level of response to the middle level of long-wavelength light. This chromatic adaptation will tend to maintain constant colours of objects under changing illumination. It will also create an imbalance in the response of the three cone types after prolonged exposure to light that stimulates primarily one cone type, thus, for example, causing a cyan after-image to appear after prolonged viewing of red light.

Spatial chromatic contrast – or simultaneous colour contrast – is another fundamental perceptual phenomenon, also hard-wired and also potentially linked to colour constancy. Chromatic contrast occurs when a surface of one colour induces its opponent colour in an adjacent surface: for example, when a small grey square 'turns' pink against a greenish background. The phenomenon is mediated by spatial interactions between neurons in the visual pathway, which are almost certainly active at all times, but the perceptual vividness of the effects varies enormously, depending on the size of the surfaces, their relative brightnesses, textures, depth and motion (Hurlbert and Wolf, 2004). Nonetheless, the effects of simultaneous chromatic contrast can be very powerful, and were striking enough for Chevreul, director of the Gobelins dye factory in the early 1800s, to observe their action on the appearance of dyed yarns and construct a quantitative theory to explain the phenomenon (Chevreul, 1855).

Thus, the colours that we see are not solely determined by the instantaneous triplet of cone responses at any one location, but also by the cone responses that have preceded these in time and which surround these in space or, in other words, by their temporal and spatial context. (There is the added complication that no one retinal location is guaranteed to contain all three cone types, because of uneven distribution of cone types between the fovea and periphery and because of packing constraints (Brainard *et al.*, 2008).) Colour is fundamentally a contextual phenomenon, dependent on the sensory information that has come before and that emanates simultaneously from the surroundings.

Given the mutability of colour – its dependence on context – it might seem remarkable that colour serves as a reliable cue for any visual task or behaviour. Indeed, certain prominent schools of art have argued that colour does not, and cannot, convey real truths in the way that form does (Kemp, 1990). Yet the very processes that cause colour to be influenced by its context are those that stabilise its meaning and ensure its usefulness. Chromatic adaptation works toward colour constancy, keeping object colours constant even while the illumination changes. Simultaneous chromatic contrast enhances the apparent differences between object and background, enabling better detection of the former. Where the background colour largely reflects the illumination spectrum, simultaneous contrast also acts to factor out the effects of the illumination, achieving object colour constancy in a similar way to temporal adaptation. Thus, both adaptation and contrast help to ensure that colour provides a valid and reliable information to the identity and material properties of objects, and thereby facilitates object recognition and characterisation.

A closer look at the particular form of colour vision we humans possess also reveals which particular behavioural tasks it has evolved to optimise. It is generally accepted that primates who evolved the modern 'red-green' subsystem from the primitive dichromatic system must have gained selective advantages from this specific form of trichromacy (Mollon, 1989). The most prevalent hypothesis is that trichromacy boosted the ability to find edible food by enhancing the discriminability of nutritious 'reddish' fruits and/or leaves against the 'greenish' background of foliage (Dominy and Lucas, 2001: Regan et al., 2001: Sumner and Mollon, 2003). It is unclear vet which of the two behaviours - frugivory or folivory - was the more important driver for evolution, but both ideas imply that the detection and consumption of food, distinguished in its colour appearance by higher L cone and lower M cone responses against the background, are crucial to the evolution of trichromatic vision. An alternative hypothesis is that the 'redgreen' subsystem evolved to enhance discrimination of emotional states and social-sexual signals (Changizi et al., 2006), via the perception of subtle changes in skin colours. Both hypotheses are supported by analyses of the spectral tuning of the 'modern' L-M channel, which is optimal both for discriminating changes in skin spectral reflectance due to changes in the haemoglobin oxygen saturation level (Changizi et al., 2006) and for discriminating edible 'reddish' or 'yellowish' targets against 'greenish' foliage (Sumner and Mollon, 2003). Trichromatic primates also tend to be more bare-faced than dichromats, consistent with need for greater visibility of the face in animals that use skin colour signalling.

The question nonetheless remains as to which of these drivers, foodfinding or social–sexual signalling, came first. Various lines of argument suggest that food-finding may have had precedence: Barton (1998) concluded from an analysis of brain volumes across 34 species that the evolution of frugivory in diurnal species coincided with an expansion of the neocortex which in turn correlates with expansion of the layers containing colour-selective cells in the thalamus; thus, as the capacity for colour vision grew, so did the ability to find fruits, suggesting that the need for the latter drove the former. From a statistical analysis of the occurrence of four main traits (pelage colour, colour vision, mating system and the presence or absence of red skin) across 203 primate taxa, Fernandez and Morris (2007) conclude that primate trichromatic vision evolved earlier than 'red' coloration of skin. This conclusion lends weight to the hypothesis that trichromacy evolved to improve foraging performance, and was later exploited through sexual selection, shaping the evolution of 'reddish' traits as well as enabling greater social complexity via enhanced visual signalling (Barton, 1998). Thus, human colour vision likely evolved in order to optimise foodfinding and was then capitalised on for other vital behaviours such as matefinding and social-sexual signalling. The fundamental nature of trichromacy and second-stage colour processing embed a natural opponency between red and green on one dimension, and blue against yellow on the other. The fundamental characteristics of temporal and spatial processing further ensure that we constantly adapt to a changing environment yet constantly recover the meaningful properties of the objects with which we interact.

5.3 Colour preference in humans

The psychology of colour preference has been widely studied for more than a century but, despite popular misconceptions, little is known about the factors that influence colour preference or its biological origins. The majority of past investigations into colour preference have been phenomenological, aiming to determine which colours individuals or populations prefer, rather than why people have preferences at all. More recently, investigators have begun to address the meaning of colour preference in terms of its evolutionary origins and biological significance.

It is natural and commonplace to think of colours as abstract attributes which exist independently of any object or surface: we readily call to mind the colours green or red, without visually attaching these to a leaf or strawberry. Likewise, we are able to view a real material thing – a piece of fabric, or a face – and visualise it being a different colour, as if we could lift off the surface colour and transform it before reapplying. One might speculate that we humans possess the ability to mentally repaint objects in different colours because we possess the ability to do so physically, by using real paint or pigments, exposing our skin to the sun, or editing images with contemporary graphics tools, for example. It might even be that the ability to abstract colour arose only after our evolutionary ancestors developed the ability to manipulate surface colour.

These speculations aside, the fact remains that colour is a perceptual quality that exists both as an object attribute and as a mental entity – it is detachable from real surfaces. The distinctions made in colour science between different 'modes' of colour – surface colours, related colours and

void colours (Beck, 1973) - are driven by this fact. The evidence from neuroscience also points to the existence of colour as an abstract quality as well as an object property. The conventional view is that at early stages of visual processing, colour is analysed by specialist brain cells independent of form. motion, and depth. Recent evidence suggests that this segregation is not complete (Gegenfurtner and Kiper, 2003), but the processes which integrate colour with these other visual attributes to form neural representations of objects, and where in the brain areas these processes occur, are still not fully understood. Furthermore, there is evidence that, even at relatively late stages of visual processing, neural representations of colour exist that are independent of representations of other attributes. Critchley (1965) described several phenomena experienced by neurological patients following lesions of the central visual pathways, in which colours would appear to free themselves 'from the confines of their objects' and spread into surrounding space. More recently, Murphey et al. (2008) demonstrated that electrical stimulation of neurons in the ventral temporal cortex of a conscious individual elicited non-localisable perceptions of a 'blue, purple color, like aluminum foil when it burns'. In a homologous inferotemporal cortical area (TE) in closely related primates, neurons, when probed electrophysiologically, show high selectivity for colour but low selectivity for shape (Conway et al., 2010). These and similar findings suggest that certain groups of neurons, even at relatively late stages in visual processing, encode colour in an abstract sense, unbound to a surface and unattached to an object.

This 'abstract-able' quality of colour is central to the prevailing ideas on the evolutionary origins of colour preference. The key point is that, given the importance of object colour in survival-critical behavioural tasks, such as finding ripe food or attractive mates, we humans will have developed preferences for those colours that signal useful or desirable properties of the objects to which they are attached. That is, a preference for objects of a particular colour will evolve into a preference for the colour itself. The desire to seek reddish berries for their edibility will evolve into a general preference for reddish contrasts against a greenish background. This evolution of colour preference out of object preference could not occur if colours were not separable from objects. It may be, of course, that the persistent, repeated need for selecting preferred objects drove the separability of colour out of a need for efficiency, streamlining the process by selecting objects on the basis of a single visual attribute, instead of on the entire complex of object properties.

This argument, that preference for coloured objects drives preference for colour, has been made implicitly or explicitly by several authors, including Humphrey (1976), Hurlbert and Ling (2007) and, most recently, Palmer and Schloss (2010). Humphrey (1976) stated that to understand the emotional

meaning that people attach to colours, one must understand the significance of what colours signal in nature. Humphrey argues that the power of red to arouse emotions, both positive and negative, lies in the ubiquity of its use as a behavioural signal, indicating edibility in berries but toxins in toadstools, sexual attractiveness in the flush of a monkey's bottom but threat in an open mouth. Hurlbert and Ling (2007) also interpret their findings on the assumption that colour vision evolved for a purpose or, more likely, various purposes, all to do with improving survival fitness: ... as foodseeking has likely influenced the evolution of trichromatic colour vision, it is natural to speculate that it may also have affected colour preference. The colours of more desirable foods may naturally be more preferred' (Ling et al., 2006). Palmer and Schloss (2010) move the argument from the phylogenetic timescale to an ontogenetic one, explicitly stating the idea that individual colour preferences may arise from emotional responses to specific objects experienced during an individual's lifetime. Their test of the 'ecological valence theory' compared average individual colour preferences with the average individual preferences for objects associated with the same colours, in a local population, and found a close correspondence.

Despite the common-sense appeal of these arguments, it is important to stress that neither the evolutionary nor the ontogenetic claim has been proven, and the extent to which preferences are hard-wired vs individually malleable is still an open question. Individual lifetime experiences may have a strong influence on colour preference (passions for football clubs may lead to passion for team colours and, likewise, local rivalries may lead to revulsions for other colours, as Newcastle and Sunderland supporters know well), but these individual variations may be built on top of underlying universal preferences which remain relatively unperturbed. Further, it is difficult to disentangle the origins of universality where they exist: common preference patterns over a population may indicate 'hard-wired' preferences established over an evolutionary timescale, or individual, plastic preferences constructed through common exposure to common stimuli that arouse common emotions – the pleasure evoked by a clear blue sky may be as common now as it was millennia ago, and any consequent preference for blue may therefore have both contemporary and ancient antecedents.

Given the importance of the behavioural uses of colour, and the known perceptual and physiological properties of colour vision, it is nonetheless logical and compelling to argue that preference for objects with colours that signal useful or desirable properties should transfer to the colours themselves. It is important, therefore, to look closely at patterns of human colour preference over time to determine whether they follow the predictions of the main hypothesis. Early studies of human colour preference were suggestive of universal tendencies, but not systematic or controlled enough to prove the point. More recent studies have demonstrated both universality and individuality, as well as mutability across culture and age.

5.3.1 Colour preference studies

History

The propensity of humans to associate emotions with colours is probably as old as poetry: Shakespeare's 'green-eyed monster' (in Othello) conveyed the repellent quality of jealousy through the colour commonly associated with it in renaissance England. Goethe (1810) wrote that with yellow 'the eye is gladdened, the heart expanded and cheered, a glow seems at once to breathe towards us.' The common fascination with colour and its emotional associations must have been a driving force for the surge in quantitative colour preference studies that began in the late 1800s and continued through the early 1900s (Chandler, 1934). Another driver was the general scientific interest in understanding the biological basis of colour perception and the limits of colour discrimination, at a time when neither of the rival theories of colour vision (Young's and Helmholtz's trichromacy theory and Hering's opponent-process theory) had been unequivocally proven.

One of the earliest documented colour preference studies was Jastrow's mass experiment conducted on 4556 visitors to the World's Columbian Exposition in Chicago in 1893 (cited in Chandler, 1934 and Dorcus, 1926). Jastrow asked individuals to vote for their single favourite colour from a set of 12 coloured paper rectangles (six primaries and six intermediate colours in the Prang series), simultaneously displayed on a large placard. The rank ordering of votes was: blue, red, light blue, blue–violet (together taking up half of the votes); followed by red–violet, light red, violet, 'no choice', green and yellow (together taking up the third quarter of votes), with the least popular colours being 'orange and its shadings toward red and yellow' (Chandler, 1934).

Jastrow's method, asking observers to select their favourite colour (or the first few favourites) from a set of test alternatives, has the twin advantages of simplicity and speed, and is still used where large population comparisons are desired (Saito, 1981, 1996; Camgoz *et al.*, 2002). Yet it provides at best very limited information on the relative strengths and ordering of preferences between colours, and no direct information on inter-individual variations. Other methods provide more accurate and detailed information. For example, rank ordering – asking observers to arrange a series of colours in the order of their preference (Eysenck, 1941; Granger, 1955; Gelineau, 1981) – provides information on the order of preferences, but not on relative strength. Rating methods instruct the observers to gauge the power of individually presented colours, and thereby generate a quantitative

representation of preference strength for each tested colour (Guilford and Smith, 1959; Helson and Lansford, 1970; Reddy and Bennett, 1985; Ling and Hurlbert, 2007; Palmer and Schloss, 2010). The most accurate, yet also most time consuming, method is to perform pair-wise comparisons for a group of colours (Dorcus, 1926; Choungourian, 1968; McManus *et al.*, 1981; Ou *et al.*, 2004; Ling *et al.*, 2006). This method generates a numeric colour preference curve for each individual subject which is less susceptible to extraneous bias, such as the tendency of observers to avoid extremes of the rating scale. Methods which use verbal stimuli, such as colour names, and request verbal reports of preferences or emotional associations, are the least accurate and reproducible (Buckalew *et al.*, 1989; Silver and Ferrante, 1995).

Most studies in the first half of the 20th century, whatever the method used, were contaminated by poor experimental control, lacking (or not specifying) calibration or replacement protocols for coloured samples vulnerable to decay, using unspecified or uncontrolled illumination and viewing conditions, and deploying unreliable methods of quantifying preference. General patterns within the individual results were therefore difficult to discern and, given the 'chaotic character of the results', Chandler (1934) refuted the notion of a universal mechanism underlying colour preference. Nonetheless, a consistent top ranking of 'blue' emerged amongst the varied observers across studies. Indeed, the similarity of preferences across populations may have stymied the aims of some studies seeking evidence for racial differences (e.g. Garth, 1922, 1924).

In the latter half of the 20th century and beyond, technical advances and more rigorous experimental control have bred a new crop of preference studies which have strengthened the evidence for an underlying universal pattern of colour preference. Preferences are consistently found to be highest in the region of blue to green and lowest in the region of yellow and yellow–green (e.g. Guilford and Smith, 1959). Eysenck's (1941) description of a general order of preference (blue, red, green, purple, orange and yellow) is remarkably similar to Jastrow's list, obtained 50 years earlier and with a more limited method, and has been largely supported by subsequent studies (Granger, 1952, 1955; Guilford and Smith, 1959; Helson and Lansford, 1970; McManus *et al.*, 1981; Camgoz *et al.*, 2002; Ou *et al.*, 2004). The most recent data from Hurlbert and Ling (2007) and Palmer and Schloss (2010) are also in broad agreement with these studies, again placing 'blue' in the most preferred position and 'greenish-yellow' in the least preferred position, on average across the populations studied.

These studies are in themselves limited as explorations of the emotional meanings and effects of colour. Mere preference may rightly be considered as only one dimension in a complex space of affective responses to colour. There is a parallel history of studies that examine wider ranging emotional associations to colours, again using a range of techniques including individual ratings (Valdez and Mehrabian, 1994) and forcedchoice comparisons (Simmons, 2011). In these studies, the 'pleasantness' or 'pleasure' dimension in emotion space correlates best with preference. For example, Simmons (2011) found, using a three-alternative forced-choice method to rate colours in the PAD (pleasure/arousal/dominance) space (Russell and Mehrabian 1977), with populations of UK undergraduates, that pleasantness was highest for purple, blue–purple and pink, and lowest for green, yellow–green and orange. The pattern mirrors both typical preference patterns, as well as earlier 'pleasure' ratings (Valdez and Mehrabian, 1994). Simmons (2011) further found that the most 'calming' colours were 'pastel blue' and lilac, and the most 'mood-lifting' saturated reds and yellows.

Yet other studies have explored the broader psychological implications of colour preference. A prevalent notion in the latter half of the 20th century, embodied in the Lüscher Colour Test (Lüscher and Scott, 1969), was that individual personality characteristics may be predicted from individual colour preferences. While many subsequent studies specifically examined the validity of the Lüscher Color Test and found it limited (Holmes *et al.*, 1986; Picco and Dzindolet, 1994), others investigated the possible link between psychophathologies and colour preference, including, for example, schizophrenia (Cernovsky and Fernando, 1988), depression (Cohen and Hunter, 1978) and anxiety (Ireland *et al.*, 1992), with mostly inconclusive results. Gelineau's (1981) study of 101 college-age subjects combined a 77-item colour sorting task with controlled lightness and hue of the samples and concluded that there was no reliable relationship between preference and personality type.

Universality and individuality of colour preference: recent studies

This seeming universality of colour preference has prompted researchers to propose mathematical formulae which predict the preference value of a given colour based only on its co-ordinate location in a standardised colour space (Ou *et al.*, 2004). These are in line with earlier studies that attempted to quantify the relative contributions of distinct colour attributes to preference (Guilford and Smith, 1959), and to determine whether the general order of either hue, saturation or brightness preference remains independent of changes in level of the other two (Granger, 1955). Such models are effectively 'standard observer' models of colour preference and do not aim to capture or analyse inter-individual variations. Yet, as other studies have made clear, not all individuals behave in the same way. The universal pattern found in the above studies is modulated by a number of factors: sex (Eysenck, 1941; Helson and Lansford, 1970; McManus *et al.*, 1981), age

(Adams, 1987; Dittmar, 2001; Pereverzeva and Teller, 2004; Bonnardel *et al.*, 2006), and also by geographical origin (Choungourian, 1968; Saito, 1981, 1996; Reddy and Bennett, 1985). An ideal preference system should thus incorporate both the individual variability as well as the universal similarities of colour preference.

In our recent studies, we proposed a novel model of colour preference, which enables us to quantify colour preference in terms of a small number of factors directly linked to the underlying neural components of colour encoding and to analyse inter-individual variations in terms of these factors (Ling et al., 2006; Hurlbert and Ling, 2007). For our primary method of testing, we used a computer-based paired-choice test with a set of eight intermediate hues at three distinct lightness-saturation level combinations, giving 24 colours in total. Observers view each possible pair (displayed as two rectangular patches either side of a central fixation area) in succession and are instructed to pick, as rapidly as possible, their preferred colour in each pair. The colour stimuli are reproducibly specified and controlled in terms of the three primary perceptual attributes of colour: hue, saturation and lightness. They are displayed on colourimetrically calibrated CRT or LCD screens as rectangular patches centrally placed on uniform neutral backgrounds and viewed in otherwise dark conditions; thus, chromatic adaptation and spatial contrast effects are controlled and constant across observations. In a secondary experiment (Ling and Hurlbert, 2007), we compared the paired-choice method with a rating method, in which each colour stimulus was displayed singly in the centre of the calibrated screen above a horizontal slider scaled from 'Dislike' to 'Like'. The observer's task was to slide the bar as quickly as possible to the position corresponding to the degree to which he/she liked the colour. The speed and efficiency of this method allowed a much greater number of colours to be tested (134 vs 24). The results of the two methods are qualitatively similar and quantitatively highly correlated, preserving both individual differences and group effects.

The hue preference curves for each of the different lightness–saturation combinations show a universally similar pattern, peaking in the bluish/ bluish-greenish region and falling towards the greenish-yellowish region. In other words, hue preference is largely maintained across different lightness–saturation combinations – i.e. bluish hues tend to be preferred to yellowish hues whether both are at the same low saturation, or both at the same high saturation – but there is also a universal tendency to prefer more saturated colours overall.

There is also significant individual variation in the hue preference curves, despite these universal tendencies. We have demonstrated that this individual variation is to a large extent captured by the variation in just two factors, the weights on the two fundamental hue encoding mechanisms: the L–M ('red'-'green') and S–(L+M) ('blue'-'yellow') cone-opponent contrast mechanisms. (The hue of each colour can be fully described by its coordinates in cone-contrast space, defined by the L–M contrast with the background and the S–(L+M) contrast with the background, ratios that are likely encoded in the activity of colour-selective neurons at early stages in visual processing (Lennie and Movshon, 2005)). For the standard set of eight colours at mid-saturation and lightness, these two components account for 70 % of the variance in individual preference patterns over 208 observers aged 20–26. (For the full set of colours, moderate improvements are gained by extending the cone-contrast model to include additional components for luminance contrast and saturation (Ling and Hurlbert 2007).)

Similarly, Palmer and Schloss (2010) found in their study of 48 observers aged 18–71, using a slider-rating method, that hue preference patterns peaked in the 'blue' range and dipped in the 'yellow'-'green' range; remained effectively the same across three lightness-saturation combinations; and that at almost every hue, colours of higher saturation were preferred. For a fourth lightness-saturation combination, 'dark' colours, the pattern of hue preferences changed significantly: dark oranges and yellows were far less preferred than their lighter counterparts (although it should be noted that hue was not held perfectly constant across different lightness levels) and dark reds and greens were more preferred than lighter reds and greens. For the core set of colours sharing the same saturation and lightness, similar to Hurlbert and Ling's standard set of eight, the cone-contrast encoding model explained 64 % of the variance in preference; for the full set of 32 colours covering a wider range of lightness and saturation levels, a different colourencoding model explained the data better than the extended cone-contrast model, accounting for 60 % of the variance. This model also decomposes colours in an opponent-colour space, but one which is almost certainly higher level in visual processing than the cone-contrast opponent space from which it derives - crucially in this space, the hue dimensions of red/ green and yellow/blue, lightness dimension of light/dark and saturation dimension of high/low are defined by observers' appearance ratings. Whether or not these dimensions correspond to the unique hue directions or other perceptually defined dimensions is a matter for further investigation which may reveal more about the neural site of preference representations.

But the best fit of the Palmer and Schloss colour preference data across all lightness–saturation combinations was given by the weighted affective valence estimates ('WAVES') of each colour. The WAVES were constructed by averaging a set of emotional response ratings provided by a different group of 98 observers (aged 18–36) for objects matching the same colours. Here, observers were asked to rate the relative appeal of individual objects, indicated by name only, again using a slider scale ranging from positive to negative. These affective ratings were weighted by the strength of the colour match between the named object and the tested colours (determined from a separate matching experiment on 31 observers, aged 18–28 years). The set of 222 objects were determined from another experiment in which 74 observers viewed individual colours and described objects associated with each. Thus, 'strawberries' may have been named as objects associated with a particular dark red colour and independently rated as positively appealing; the affective valence estimate for this dark red colour would then have been assigned a positive value, modulated by how strongly it matched other observers' memory colour for strawberries, and by the valences accorded to other objects matching the same dark red.

These findings strongly support the notion that colour preferences are derived from preferences for objects with the corresponding colours, and that these preferences are deeply embedded. This study demonstrates that across a range of ages, object preferences and their colour associations are similar, as are colour preferences which, in turn, accord with the universal colour preference pattern emergent from past studies. That these colour preferences are also explained well by differential weightings on perceptual colour-encoding mechanisms supports the notion that colour preferences may be instantiated in neural mechanisms laid down over millennia, that our opposing emotional responses to blues and yellows resonate with their opponency in neural encoding, and are accordingly strengthened and streamlined.

5.3.2 Sex differences in colour preference

Despite the universality in colour preference, significant differences between individuals and groups have also emerged, repeatedly but not always consistently. Sex differences in colour preference are one of the most controversial variations, both difficult to prove statistically and, where discovered, difficult to disentangle from other factors. For example, other variations, such as age (see section below) may mask or enhance the effects of sex. Jastrow (1897) was the first to report a sex difference in colour preference: although blue overall received the most votes over the entire population studied, women (N = 1810) were nearly twice as likely as men (N = 2746) to choose red as their single most preferred colour, with a red:blue preference ratio of 1.25. The imbalance in numbers of women and men, together with lack of information about their ages and other biographical information, makes it difficult to interpret the finding conclusively as a difference due to sex.

Where sex differences have been reported, they are of two main types: the first is a difference in the ranking of preferred colours; the second, more often and consistently demonstrated, is a difference in the degree of

preference, its stability and its reliability. In general, females are reported to have stronger preferences than males, varving more profoundly between hues, as well as greater stability of preferences over short timescales. There is a female bias towards red, which emerges from differences in rankings as well as differences in depth of preference. For example, in his comprehensive and relatively well-controlled study, Dorcus (1926) found stronger preferences (greater 'pull' of preferred colours) for females than males, both in children aged 8–10 (150 boys: 147 girls) and in college-age men (430) and women (401). Although there was 'little difference' in preference rankings, the data reveal the strongest difference to be for reds, with females showing higher preference rankings, and for yellows and oranges, with males showing higher preference rankings. McManus et al. (1981) also found that although both sexes were more likely to prefer blue and to dislike red and yellow, of those who preferred red or yellow, significantly more were female. The female dislike for yellow was also more pronounced, compared to males. Guilford (1934) found that female affective-value ratings of colour were more difficult to predict using a simple interpolation model, unlike male responses which tended to be higher and more uniform. Gelineau (1981) found that females show significantly greater stability of preference over a timescale of five weeks.

With respect to differences in preference rankings, Evsenck (1941) found minor sex differences involving orange and yellow, while Granger (1955) concluded that there was no evidence of any marked differences between men and women. On the other hand, Helson and Lansford (1970) reported significant sex differences for 'pleasantness' ratings of Munsell chips under several different illumination conditions, with females rating R, YR and Y chips higher than males, and males rating B, BP and RP chips higher than females. Sinha et al. (1970) reported that female adolescents ranked red higher than did male adolescents, in India; Saito (1996) found that young adult Japanese females highly preferred 'pale pink', whereas males did not. Yet more recent preference studies have found no significant sex differences (Camgoz et al., 2002; Ou et al., 2004), and some earlier studies found that men had higher preference for red than women (Silver et al., 1988). One important caveat to note is that the 'red' tested in these diverse studies varies considerably both in saturation and lightness, and it may be that any sex difference that does exist depends not only on hue, but also on the other two attributes. Indeed, we found a significant sex difference in overall lightness preference, with UK females preferring lighter colours and UK males showing no preference for lightness.

In our analysis of hue preference (Hurlbert and Ling, 2007), we found a significant difference between male and female weights on the L–M ('red'– 'green') cone-contrast components across both Chinese and UK population samples (N = 161 and 37 respectively, aged 20–26), with females according

significantly more positive weights to the 'red' end of the axis. Thus, females showed stronger preference than males for colours with a 'reddish' contrast against the background. Both sexes in both sub-populations, though, gave positive weight to the 'blue' end of the 'blue'-'yellow' axis, lending further support to the notion of a universal preference for 'blue'. Further, we found that female colour preferences are more pronounced: the overall variation in preference across different hues was significantly higher for females than males, for the UK population.

One speculation – and it is important to stress that this is speculation, not proven – is that a bias for reddish objects may have arisen from the bias for ripe fruits and leaves against inedible green backgrounds, at the time when fruit-finding drove the development of modern trichromacy (Barton 1998; Regan *et al.*, 2001). We may further speculate that this bias may be more likely to appear in females because of greater specialisation of the female brain for foraging-related tasks, a notion supported by studies of visual spatial abilities (Kimura 1992; Eals and Silverman, 1994; McBurney *et al.*, 1997; McGivern *et al.*, 1997; Dabbs *et al.*, 1998). The greater certainty and stability in female colour preference would support the notion that females are more attentive to colour information because of its necessity in certain behavioural tasks.

There are also sex differences in coloration which may influence sex differences in preference. For example, males have 'ruddier' complexions than females, and this sex difference arises at puberty and is universal across races (Frost, 1994; Nestor and Tarr, 2008). If sexual selection is also a driver for colour preference, then it may be that females naturally prefer redder faces, and this preference may be ingrained in the tendency to give positive weighting to the L–M contrast component that we see here. Alexander (2003) argues that female preference for 'reddish-pink' might be related to reproductive advantage, because infant faces also tend to be pinker than average.

5.3.3 Age differences and the development of colour preference

A potentially confounding factor in all studies examining similarities and differences in preference across populations, particularly those due to sex, is age. It has become increasingly clear that development and ageing influence colour preference, in a way not entirely explained by changes in colour vision, linguistic ability or other cognitive factors. As early as 1926, Dorcus acknowledged that colour preferences changed with age, and admirably summarised the existing scientific evidence. He reported that Holden and Bosse (1900; cited in Dorcus, 1926) found that the 'order of preference develops from the red towards the blue end of the spectrum as the child

grows older', whereas Havelock Ellis (1900; 1906; in Dorcus, 1926) concluded that children's preferences were 'decidedly' influenced by colour associations they formed at the time. Dorcus' own systematic study (1926), of 1235 individuals from five different main age groups, found that more 'decided' preferences occurred in the college-age groups, compared with both the younger (8, 9 and 10 years) and older (greater than 60 years) groups. In the elderly group, preferences were generally diminished, but a sex difference emerged in that females had significantly higher preferences for 'purple' than did males, and placed it in 'first position'.

More recently, Dittmar (2001) compared the responses of younger (age 19–44) and older (52–90) Germans when asked to choose their most and least favourite colours out of four given names (blue, green, red and yellow). The results illustrated that although blue was universally preferred by all ages, the preference for blue decreased steadily with advancing age and the popularity of green and red increased. Bonnardel *et al.* (2006) examined colour preference of 21 Munsell samples, for 20–30 and 60–70 year-old subjects, using the method-of-triads (i.e. to indicate the preferred colour among three samples in a series of presentations), and found that the sex differences in colour preference were significantly reduced for elderly subjects compared with young adults.

In a separate study of colour preference across different age groups and both sexes in the UK (Ling and Hurlbert, 2011), we found no main effect of age, or in other words, the average preference pattern varied little between the age groups. But the sex difference varied significantly, being most magnified for the 11-12 year-olds - with girls having higher preference in the 'purple' and 'red-purple' region than boys, and boys having higher preference in the 'green' and 'green'-'yellow' region than the girls - although still significant for both 8-9 year-olds and 18-22 year-olds. For 61-88 yearolds, the sex differences effectively vanish, in agreement with Bonnardel et al. (2006). These changes are summarised in the changes of the weights on the L-M component: at age 11-12 years of age, the L-M weights are at their most positive for girls and most negative for boys, whereas at age 61-88 years, the L-M weights are negative for both males and females and statistically indistinguishable. Further analysis reveals that the reduction in sex difference is almost entirely due to long-term changes in the female preference pattern: there is a significant difference in female hue preference patterns between ages 11-12 and 61-88, but none for the males. (Note that this finding is not inconsistent with female preference patterns being more reliable than males on a shorter timescale.)

Poorer colour discrimination in old age, induced by changes in the spectral characteristics of the lens (Sagawa and Takahashi, 2001; Knoblauch *et al.*, 2001) may account for the overall flattening of the hue preference pattern for the elderly age group in comparison with the younger age groups, but cannot account for the reduction in sex difference. The latter may instead be caused by biological factors such as differences in the rate of decline of sex hormone levels with age between males and females, or by environmental or social factors which are yet to be teased apart.

The lack of sex differences in colour preference in the elderly is mirrored by a similar lack in infancy. Although hue preferences – measured as looking times and with care taken to control for extraneous factors such as brightness (e.g. Teller *et al.*, 2004; Zemach *et al.*, 2007) – have been demonstrated in infants as young as 3 months of age, sex differences in preference have not been reported. Studies also disagree as to which hues are most preferred by infants. While most concur that 'green' and 'yellow-green' are looked at least, and 'blues' and 'reds' are most preferred, the order differs somewhat across all studies (Bornstein, 1975; Adams, 1987; Zemach *et al.*, 2007), a fact which may be partly explained by differences in stimuli and notation (Zemach *et al.*, 2007).

To eliminate uncertainty in stimulus specifications, Franklin *et al.* (2010) used the same stimuli as for the adult studies by Hurlbert and Ling (2007) and found that infants of 4–5 months had higher preference for reddish hues and lowest preference for greenish hues. There was no sex difference: the L–M cone-contrast component explained 40 % of the variance in the individual data overall, with both males and females weighting it positively. The very early preference for positive L–M contrast in both sexes is consistent with other findings on the salience of 'red'. For example, models of the evolution of colour lexicons predict that the first colour word to be acquired by a language (after 'black' and 'white') would be 'red' (e.g., Berlin and Kay, 1969), although evidence for the primacy of red in individual language development is lacking (Pitchford and Mullen, 2005).

Taken together, the variation in colour preference from infancy to old age suggests that neither absolute colour preferences nor sex differences in colour preference are hard-wired from birth. Instead, colour preferences and sex differences develop and change over time. These changes in preference may in turn be driven by hard-wired predispositions which are moulded by other biological and developmental factors - such as the maturation of conceptual frameworks for colours (see e.g. Sandhofer, 2006) or levels of sex hormones - or by environmental factors. For example, the positive response to blue may emerge fully only after natural exposure and experience, and innate tendencies to prefer red may be exaggerated by feedback from the social environment. Preferences may also be learned through associations with objects, and as interactions change through time, so new associations may be acquired and older ones diminished. There is strong evidence, though, that the ability to form emotional associations to colour, whether on an ontogenetic or evolutionary timescale, is deeply embedded in human nature.

5.4 Colour preference in animals

Although the biological origins and evolutionary drivers of colour preference in humans have been relatively unexplored and are still debated, the story is different for other animals, and highlights important areas for further study in humans.

The question of nature versus nurture in the origins of colour preference is easier to address in other animals, where experience can be tightly controlled from the moment of birth. Exploiting rigorous control of the environment, researchers have been able to demonstrate innate colour preferences in several species, including butterflies, bumblebees and mice. For example, newly emerged hoverflies with no prior experience of flowers will approach and attempt to feed from artificial flowers of only one spectral type – those which have the same spectral reflection characteristics as pollen, and to humans appear yellow (Lunau and Maier, 1995). Other flower-visiting species show similarly strong innate colour preferences: naïve pipevine swallowtail butterflies also exhibit a colour preference for yellow (Weiss, 1997) and bumblebees (Bombus terrestris) show strong biases towards violet (Raine and Chittka, 2005, 2007). Innate colour preferences have also been claimed for rodents and primates, although the evidence is inconclusive. For example, laboratory mice, Mus musculus, evince highly significant preferences for cage colours, irrespective of their home cage colour (Sherwin and Glen, 2003), white cages being the most preferred and red the least but, given the putative primitive dichromacy of mice, the preference may be explained by brightness rather than colour differences. Wells *et al.* (2008) report that gorillas (N = 6) and chimpanzees (N = 6)display preferences for blue and green objects over red objects (for both manipulable objects - cloths and boxes - and non-manipulable objects coloured transparencies fixed to windowed walls). The results may be confounded by prior experience of coloured objects which affected the perceptual novelty of the test objects, and the authors also speculate that the red objects might have been not merely less preferred but actively aversive.

Animal studies also offer us unique insight into the relationship between innate colour preference and ecological advantages, as well as their interaction with environmental factors such as training and rewards. Raine and Chittka (2005, 2007) have shown that bumblebees' innate colour preference for 'violet' reflects the traits of local flowers that are most profitable for them (e.g. highest in nectar and pollen rewards), and bees with the strongest bias for 'violet' in the laboratory also harvest more nectar in the field. Innateness, nevertheless, is not the only factor influencing animal colour preference. While domestic chicks (*Gallus gallus*) innately prefer 'orange' to 'blue' (Ham and Osorio, 2007), their colour preferences have also been

shown to be affected by their visual environment (Miklosi *et al.*, 2002). The preference for 'orange' objects is reduced or abolished for chicks raised in an environment dominated by 'blue' objects. Bumblebee colour preference is also susceptible to environmental manipulations: when test colours are similar to the colour on which the bees have been extensively trained, the bees choose colours according to their similarity to the trained colour. But when the test colours differ significantly from the trained colour, the bees' choices are more affected by their innate colour preference (Gumbert, 2000). These studies provide compelling evidence for the interaction between innate colour preference, training and learning. Lessons may be drawn for human colour preference for the dual influence of evolutionarily hard-wired factors and learned associations.

In a series of classic experiments, Humphrey and colleagues (Humphrey 1971, 1972; Humphrey and Keeble, 1977) found that monkeys preferred 'blue' light over 'red' light. The setup is crucial to interpreting the findings: here the monkeys viewed a large screen in an otherwise dark room, and selected the full-field colour projected onto the screen in a paired choice experiment. Blue was chosen more often when paired with either red or white (of equal brightness). Humphrey and colleagues ultimately interpreted these findings not as revealing sensory preferences, but instead as having an effect on the monkey's subjective timing. This conclusion was strengthened by a second experiment in which monkeys were allowed to move freely between two otherwise enclosed chambers bathed in coloured light. Here the monkeys showed no preference for one light colour over another but, when both chambers were illuminated by red light, monkeys moved more frequently, between the two chambers, as if their subjective clocks were speeded up (Humphrey and Keeble, 1978). Thus, the apparent preference for blue over red was explained by a tendency to seek change more in a red environment, and seek change less in a blue environment.

This alternative, persuasive interpretation of what began as an exploration of colour and brightness preferences highlights another complication in reconciling and understanding results of different studies. Particularly in animal colour preference experiments, it is important to distinguish between target colours vs field colours, and between object colours vs light colours. In simple terms, a preference for reddish objects against greenish backgrounds may also imply a preference for greenish backgrounds, which must not then be misconstrued as a preference for greenish objects; therefore, colour preferences may depend on the size of the test target and whether it constitutes the foreground or background. Likewise, a preference for a particular light spectrum (e.g. long-wavelength dominated light) illuminating the entire scene does not necessarily imply a preference for small objects reflecting the same spectrum of light. The extent of chromatic adaptation will be far greater for full-field colour than for small targets, whereas chromatic contrast will more greatly influence the colour of small targets. There is also other evidence to suggest that the physiological effects of fullfield illumination of different spectra may be qualitatively and quantitatively different from the emotional associations aroused by objects of different colour.

5.5 Physiological effects of background and illumination colours: 'warm' vs 'cool' colours

Humphrey's conclusion that monkeys generally accelerated their environmental sampling when bathed in red light is consistent with the prevailing notion in lighting and interior design that red excites and blue calms. It also echoes the 'warm'/'cool' distinction articulated by Lüscher and Scott (1969): '... red represents an energy-expanding physiological condition. It speeds up the pulse, raises blood pressure and increases the respiration rate. It is the expression of vital force ...' whereas 'blue has a pacifying effect on the central nervous system'.

The prevalent explanation for the calming, appeasing effects of blue light is that it projects an infinite distance like the sky; the air scatters short wavelengths of light more than long wavelengths, so more distant objects appear bluer; reasoning on past experience, our visual systems then interpret bluer surfaces as being further away. But why should expanding space pacify the soul? Again, we may invoke an evolutionary explanation that harks back to our ancestors' days on the open savannah, where clear blue sky signalled daytime, beneficent weather and lack of visible danger. But the effects of 'coloured' light on emotions and mood are also not necessarily only visual, if at all.

In addition to the classical photoreceptors in the retina - the three cone types which underpin the visual perception of colour that forms the focus of this chapter, and the rods, which exist in only one spectral type and are responsible for vision at low light levels - other light-sensitive cells exist which project to non-visual areas of the brain. These retinal ganglion cells contain a particular photopigment - melanopsin - which is maximally sensitive to wavelengths of light around 420-480 nm, shorter than the rod sensitivity peak and close to the S cone peak. Melanopsin-containing RGCs collect information about the overall level and type of light – not the spatial details of the image - and send their signals to brain areas involved in setting the circadian rhythm (e.g. the suprachiasmatic nucleus) and processing emotions (e.g. the amygdala), as well as to directly visual areas (Vandewalle et al., 2007). Activation of the melanopsin-containing RGCs thus potentially mediates a range of emotional effects, including alertness, arousal and calmness, and also modulates visual perception which, in turn, invokes emotional responses through the content of the image.

Indeed, short-wavelength, or 'blue', light has been shown to influence both emotions (short-term responses to external stimuli) and mood (longerlasting emotional state) (Viola *et al.*, 2008). For example, in light therapy for seasonal affective disorder, the mood change associated with winter darkness, blue light is as effective as white light, even when it is less bright (Anderson *et al.*, 2009). Brain imaging studies have shown that short bursts of blue light optimised for the peak of the melanopsin response (473 nm) increase activity in brain areas involved in emotions (hippocampus and amygdala) and in alertness and arousal (thalamus and brainstem) (Vandewalle *et al.*, 2007), while ambient blue light (473 nm) influences brain responses to emotional stimuli (angry voices) more than does green light (527 nm).

Thus, the 'calm' induced by 'blue' light may come about through a different route, in comparison with the pleasure experienced and preference expressed for 'blue' objects, although there may be cross-talk and ultimate convergence between the two pathways. Likewise, there may be different routes for the emotions and moods elicited by 'red'. Humphrey observed that the monkeys' activity elicited by red light was akin to anxiety, a negative mood, yet in emotional ratings red is often associated with positive arousal - 'warm' not 'cool', and 'active' not 'passive'. Elliott and Maier (2007) hypothesised that red is learned as a danger signal because of its man-made associations - stop signs, fire alarms, and error corrections - and demonstrated that brief sight of red text or figures impaired individual's performance on subsequent tests, consistent with the notion that red induces a fear of failure in an 'achievement context'. But in other studies, red has been found to improve performance, consonant with Lüscher and Scott's interpretation: 'Red is the urge to achieve results, to win success, it is the impulse towards sport, struggle, sex and competition.' For example, in competitive sports, contestants wearing red are more likely to win than those wearing other colours (Hill and Barton, 2005). Red environments (e.g. redpainted offices) induce better performance on some tasks than white or green environments (Kwallek et al., 2007). Again, the differences in measured effects may be due to differences in the form that red is presented: foreground vs background, or object vs illumination.

The discrepant findings may also be explained by alternative interpretations of the data: the red-shirt effect may be due to impaired performance of the contestant who does not wear red but views red on the other contestant, rather than improved performance of the latter (Elliott and Maier, 2007). Mehta and Zhu (2009) argue instead that the radical differences in effect are determined by the differences in the tasks; the nature of the task determines the nature of the effect. In detail-oriented tasks, such as proofreading, red backgrounds induced better performance than blue backgrounds, whereas for tests of creativity, such as word associations, blue backgrounds induced better performance than red (Mehta and Zhu, 2009). As a unified explanation, Mehta and Zhu (2009) posit that red provokes avoidance and blue elicits approach, because of their differing native associations. Red is linked to danger, and so induces the desire to avoid risk. Blue signals an open, peaceful environment, and so encourages approach and experimentation with new solutions. The avoidance motivation leads to poor performance when it quashes attempts to answer harder questions, as in the study of Elliott and Maier (2007), and leads to better performance when it elicits greater attention to detail. This explanation is plausible but does not fit all tests. Simpler explanations of the data might be as effective. The improvement in proof-reading with red backgrounds, for example, may be the result of increased contrast and/or legibility of the text. The detrimental effect of red targets in other tasks may be due to the distraction caused by their salience. Yet other evidence also suggests that the preference for red exhibited by infants is context-dependent: preferences are diminished by 'hostile' contexts and enhanced by 'friendly' contexts (Maier et al., 2009).

Putting aside methodological questions and accepting the premise that red evokes emotions and behaviours which may be negative or positive, depending on the task and context, the common element is that red elicits activity. In fruit-picking, red is the target; it attracts attention and instigates a picking response. When red is the field or the illumination, it may enhance alertness and preparedness to move in response to other stimuli.

And at the heart of all explanations is the key idea that red elicits activity because of the meaning it has acquired through prior associations: red is a salient colour because the red objects we have known demand attention and response, whether these are desirable ripe fruits or body parts, or toxic organisms to be avoided. Red light may signal sunset or fire. Because of its natural associations, our emotional response to red may be deeply embedded. Because of its man-made associations, our emotional response to red may be modified and harnessed. Because of our ability to abstract colours from the objects which confer their meanings, we are able to imbue colours themselves with meanings. Colours become effective stimuli in their own right and elicit preferences, complex emotional responses, and behaviours.

5.6 Conclusions

The universality of our attraction to blues and reds and dislike for yellows and yellow–greens suggests that colour preferences may have been driven by the fitness needs of our evolutionary ancestors. Preferences for meaningful objects of particular colour evolved into preferences for the particular colours themselves. The individuality of colour preference, on the other hand – the variations with age, sex and culture – suggests that we develop new preferences as a result of individual lifetime experiences. Our ability to learn colour preferences makes fitness sense, too, if preferences for colour streamline decision-making by enabling us to collapse the complex properties of meaningful objects into a single, simple visual cue. The ability to learn to abstract colour from objects and to associate emotional responses directly to colour is therefore likely to be 'hard-wired', whether or not particular associations are. Because colours are capable of carrying complex meanings in a single, simple visual cue, they are also consciously and collectively adopted as symbols, for team membership, cultural rituals, signs and signals. In turn, their use as societal symbols may further manipulate the emotional meaning they convey to individuals.

5.7 References

- Adams R J (1987) An evaluation of color preference in early infancy, *Infant Behav Dev*, **10**(2), 143–150.
- Alexander G M (2003) An evolutionary perspective of sex-typed toy preferences: Pink, blue, and the brain, *Arch Sex Behav*, **32**(1), 7–14.
- Anderson J L, Glod C A, Dai J, Cao Y and Lockley S W (2009) Lux vs. wavelength in light treatment of Seasonal Affective Disorder, *Acta Psychiatr Scand*, **120**, 203–212.
- Barton R A (1998) Visual specialization and brain evolution in primates, *Proc R Soc Lond B Bio Sci*, **265**(1409), 1933–1937.
- Beck J (1973) Surface Color Perception, Cornell University Press.
- Berlin B and Kay P (1969) *Basic Color Terms*, Berkeley CA, University of California Press.
- Bonnardel V, Harper L, Duffie F and Bimler D L (2006) Gender differences in colour preference: Men are more predictable than women, *Perception*, **35**, 187a.
- Bornstein M H (1975) Qualities of color vision in infancy, *J Exp Child Psycho*, **19**, 401–419.
- Bowmaker J K (1998) Evolution of colour vision in vertebrates, Eye, 12, 541-547.
- Brainard D H, Williams D R and Hofer F (2008) Trichromatic reconstruction from the interleaved cone mosaic: Bayesian model and the color appearance of small spots, *J Vis*, **8**, 5, 15.
- Buckalew L W, Buckalew N M and Ross S (1989) Note on color preference and color vision test performance, *Perceptual and Motor Skills*, **69**(3), 1039–1042.
- Camgoz N, Yener C and Guvenc D (2002) Effects of hue, saturation, and brightness on preference, *Color Res App*, **27**(3), 199–207.
- Cernovsky A A and Fernando L M D (1988) Color preference of ICD-9 schizophrenics and normal controls, *Percept Motor Skills*, **69**, 159–162.
- Chandler A R (1934) *Beauty and Human Nature*, New York: Appleton-Century-Crofts.
- Changizi M A, Zhang Q and Shimojo S (2006) Bare skin, blood and the evolution of primate colour vision, *Biol Lett*, **2**, 217–221.
- Chevreul M E (1855) *The principles of harmony and contrast of colours, and their applications to the arts* (2nd edn). London: Longman, Brown, Green, and Longmans.

- Choungourian A (1968) Color preferences and cultural variation, *Perceptual and Motor Skills*, **26**, 1203–1206.
- Cohen E and Hunter I (1978) Severity of depression differentiated by a color selection test, *Am J Psychiatry*, **135**, 611–613.
- Conway B R, Chatterjee S, Field G D, Horwitz G D, Johnson E N, Koida K and Mancuso K (2010) Advances in color science: from retina to behavior, *J Neurosci*, **30**(45), 14955–14963.
- Critchley M (1965) Acquired anomalies of colour perception of central origin, *Brain* **88**, 711–724.
- Dabbs J M, Chang E L, Strong R A and Milun R (1998) Spatial ability, navigation strategy, and geographic knowledge among men and women, *Evolution and Human Behavior*, **19**(2), 89–98.
- Dittmar M (2001) Changing colour preference with ageing: A comparative study on younger and older native Germans aged 19–90 years, *Gerontology*, **47**, 219–226.
- Dominy N J and Lucas P W (2001) Ecological importance of trichromatic vision to primates, *Nature*, **410**(6826), 363–366.
- Dorcus R N (1926) Colour preferences and colour associations, *Journal of Genetic Psychology*, **33**, 399–434.
- Eals M and Silverman I (1994) The hunter-gatherer theory of spatial sex-differences: Proximate factors mediating the female advantage in recall of object arrays, *Ethology and Sociobiology*, **15**(2), 95–105.
- Elliot A J and Maier M A (2007) Color and psychological functioning. Current directions in Pyschological Science, 16(5), 250–254.
- Eysenck H J (1941) A critical and experimental study of color preference, *American Journal of Psychology*, **54**, 385–391.
- Fernandez A A and Morris M R (2007) Sexual selection and trichromatic color vision in primates: Statistical support for the preexisting-bias hypothesis, *The American Naturalist*, **170**(1), 10–20.
- Franklin A, Bevis L, Ling Y and Hurlbert A C (2010) Biological components of colour preference in infancy, *Developmental Science*, **13**(2), 346–354.
- Frost P (1994) Preference for darker faces in photographs at different phases of the menstrual cycle Preliminary assessment of evidence for a hormonal relationship, *Perceptual and Motor Skills*, **79**(1), 507–514.
- Garth T R (1922) The color preferences of five hundred and fifty-nine full-blood Indians, *J Exp Psychol*, **5**, 392–418.
- Garth T R (1924) A color preference scale for one thousand white children, *J Exp Psychol*, **7**, 233–241.
- Gegenfurtner K R and Kiper D C (2003) Color vision, Annu Rev Neurosci, 26, 181–206.
- Gelineau E P (1981) A psychometric approach to the measurement of color preference, *Perceptual and Motor Skills*, **53**(1), 163–174.
- Goethe J W von (1810) *Theory of Colours* [trans. Eastlake C L, 1840], London: John Murray.
- Granger G W (1952) Objectivity of colour preference, Nature, 170, 778–780.
- Granger G W (1955) An experimental study of colour preferences, *The Journal of General Psychology*, **52**, 3–20.
- Guilford J P (1934) The affective value of color as a function of hue, tint and chroma, *Journal of Experimental Psychology*, **17**, 342–370.

- Guilford J P and Smith P C (1959) A system of color-preference, *American Journal* of *Psychology*, **72**, 487–502.
- Gumbert A (2000) Color choices by bumble bees (Bombus terrestris): innate preferences and generalization after learning, *Behavioral Ecology and Sociobiology*, 48, 36–43.
- Ham A D and Osorio D (2007) Colour preferences and colour vision in poultry chicks, *Proceedings: Biological Sciences*, **274**(1621), 1941–1948.
- Helson H and Lansford T (1970) The role of spectral energy of source and background color in the pleasantness of object colors, *Applied Optics*, **9**:1513–1562.
- Hering E L (1878) *Outlines of a theory of the light sense* [trans Hurvich L and Jameson D, 1964], Cambridge MA: Harvard University Press.
- Hill R A and Barton R A (2005) Red enhances human performance in contests. *Nature*, **435**(7040), 293.
- Holmes C B, Buchanan J A, Dungan D S and Reed T (1986) The Barnum effect in Luescher color test interpretation, *J Clin Psych*, **42**, 133–136.
- Humphrey N K (1971) Colour and brightness preferences in monkeys, *Nature*, **229**, 615–617.
- Humphrey N K (1972) Interest and pleasure: Two determinants of a monkey's visual preferences, *Perception*, **1**, 395–416.
- Humphrey N K (1976) The colour currency of nature, in Porter T and Mikellides B (eds), *Colour for Architecture*, London: Studio-Vista, 95–98,
- Humphrey N K and Keeble G R (1977) Do monkeys' subjective clocks run faster in red light than in blue?, *Perception*, **6**, 7–14.
- Humphrey N K and Keeble G R (1978) Effects of red light and loud noise on the rate at which monkeys sample the sensory environment, *Perception*, **7**, 343–348.
- Hurlbert A (1997) Primer: colour vision, Current Biology, 7(7), R400–R402.
- Hurlbert A C and Ling Y (2007) Biological components of sex differences in color preference, *Current Biology*, **17**(16), 623–625.
- Hurlbert A and Wolf K (2004) Color contrast: a contributory mechanism to color constancy, *Progress in Brain Research*, **144**, 147–160.
- Ireland S R, Warren Y M and Herringer L (1992) Anxiety and color saturation preference, *Perceptual and Motor Skills*, **75**(2), 545–546.
- Jacobs G H (1993) The distribution and nature of colour vision among the mammals, *Biol Rev*, **68**, 413–471.
- Jastrow J (1897) The popular aesthetics of color, *Popular Science Monthly*, **50**, 361–368.
- Kemp M (1990) The Science of Art, New Haven CT: Yale University Press.
- Kimura D (1992) Sex differences in the brain, Scientific American, 266, 81-87.
- Knoblauch K, Vital-Durand F and Barbur J L (2001) Variation of chromatic sensitivity across the life span, *Vision Research*, **41**(1), 23–36.
- Kwallek N, Soon K and Lewis CM (2007) Work week productivity, visual complexity, and individual environmental sensitivity in three offices of different color interiors, *Color Research and Application*, **32**(2), 130–143.
- Lennie P and Movshon J A (2005) Coding of color and form in the geniculostriate visual pathway (invited review), J Opt Soc Am A, 22, 2013–2033.
- Ling Y and Hurlbert A C (2007) A new model for color preference: universality and individuality, *Proceedings of the 15th Color Imaging Conference*, Albuquerque, November 5–9, pp. 8–11.

- Ling Y and Hurlbert A C (2011) Age-dependence of colour preference in the UK population, in Kay C and Biggam C P (eds), *Progress in Colour Studies 3*, Amsterdam: John Benjamins, in press.
- Ling Y, Hurlbert A C and Robinson L (2006) Sex differences in colour preference, in Pitchford N J and Biggam C P (eds), *Progress in Colour Studies 2: Cognition*, Amsterdam: John Benjamins, 173–188.
- Lunau K and Maier E J (1995) Innate colour preference of flower visitors, *Journal* of Comparative Physiology, A: Neuroethology, Sensory, Neural, and Behavioral Physiology, **177**(1), 1–19.
- Lüscher M and Scott I (1969) The Luscher Color Test, New York: Random House.
- Maier M A, Barchfeld P, Elliot A J and Peckrun R (2009) Context specificity of implicit preferences: the case of human preference for red. *Emotion*, **9**(5), 734–738.
- McBurney D H, Gaulin S J C, Devineni T and Adams C (1997) Superior spatial memory of women: Stronger evidence for the gathering hypothesis, *Evolution and Human Behavior*, **18**(3), 165–174.
- McGivern R F, Huston J P, Byrd D, King T, Siegle G J and Reilly J (1997) Sex differences in visual recognition memory: Support for a sex-related difference in attention in adults and children, *Brain and Cognition*, **34**(3), 323–336.
- McManus I C, Jones A L and Cottrell J (1981) The aesthetics of colour, *Perception*, **10**, 651–666.
- Mehta R and Zhu R (2009) Blue or red? Exploring the effect of color on cognitive task performances. *Science*, **323**(5918), 1226–1229.
- Miklosi A, Gonda Z, Osorio D and Farzin A (2002) The effects of the visual enviroment on responses to colour by domestic chicks, *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, **188**, 135–140.
- Mollon J D (1989) 'Tho she Keeld in that Place where they Grew....' The uses and origins of primate color-vision, *Journal of Experimental Biology*, **146**, 21– 38.
- Murphey D K, Yoshor D and Beauchamp M S (2008) Perception matches selectivity in the human anterior color center, *Current Biology*, **18**(3), 216–220.
- Nathans J (1999) The evolution and physiology of human color vision: Insights from molecular genetic studies of visual pigments, *Neuron*, **24**(2), 299–312.
- Neitz J, Carroll J and Neitz M (2001) Colour vision: almost reason enough for having eyes, *Optics and Photonics News*, **12**, 16–22.
- Nestor A and Tarr M J (2008) Gender recognition of human faces using color, *Psychological Science*, **19**(12), 1242–1246.
- Ou L C, Luo M R, Woodcock A and Wright A (2004) A study of colour emotion and colour preference Part III: Colour preference modeling, *Color Research and Application*, **29**(5), 381–389.
- Palmer S E and Schloss K B (2010) An ecological valence theory of human color preference, *Proc Nat Acad Sci*, **107**(19), 8877–8882.
- Pereverzeva M and Teller D Y (2004) Infant color vision: Influence of surround chromaticity on spontaneous looking preferences, *Visual Neuroscience*, **21**(3), 389–395.
- Picco R D and Dzindolet M T (1994) Examining the Lüscher color test, *Perceptual* and Motor Skills, **79**(3), 1555–1558.

- Pitchford N J and Mullen K T (2005) The role of perception, language, and preference in the developmental acquisition of basic color terms. *Journal of Experimental Child Psychology*, **90**(4), 275–302.
- Raine N E and Chittka L (2005) Colour preference in relation to the foraging performance and fitness of the bumblebee, *Uludag Bee Journal*, **5**(4), 145–150.
- Raine N E and Chittka L (2007) The adaptive significance of sensory bias in a foraging context: Floral colour preferences in the bumblebee bombus terrestris, *PLoS ONE*, **2**(6), 1–8.
- Reddy T V and Bennett C A (1985) Cultural differences in color preferences, In *Proceedings of the Human Factors Society*, **29**(6), 590–593.
- Regan B C, Julliot C, Simmen B, Vienot F, Charles-Dominique P and Mollon J D (2001) Fruits, foliage and the evolution of primate colour vision, *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, **356**(1407), 229–283.
- Russell J A and Mehrabian A (1977) Evidence for a three-factor theory of emotions, *Journal of Research in Personality*, **11**, 273–294.
- Sagawa K and Takahashi Y (2001) Spectral luminous efficiency as a function of age, Journal of the Optical Society of America A, Optics, image science, and vision, 18(11), 2659–2667.
- Saito M (1981) A cross-cultural survey on colour preference, *Bulletin of the graduate division of literature of Waseda University*, **27**, 211–216.
- Saito M (1996) A comparative study of color preference in Japan, China and Indonesia, with emphasis on the preference for white, *Perceptual and Motor Skills*, **83**(1), 115–128.
- Sandhofer C M (2006) Taking the task seriously: Reflections on measures of colour acquisition, *Journal of Experimental Child Psychology*, **94**(4), 344–348.
- Sherwin C M and Glen E F (2003) Cage colour preferences and effects of home cage colour on anxiety in laboratory mice, *Animal Behaviour*, **66**, 1085–1092.
- Silver N C and Ferrante R (1995) Sex differences in color preferences among an elderly sample, *Perceptual and Motor Skills*, **80**, 923–930.
- Silver N C, McCulley W L, Chambliss L N, Charles C M, Smith A A, Waddell W M and Winfield E B (1988) Sex and racial differences in color and number preferences, *Perceptual and Motor Skills*, **66**(1), 295–299.
- Simmons D R (2011) Colour and emotion, in Kay C and Biggam C P (eds), *Progress in Colour Studies 3*, Amsterdam: John Benjamins, in press.
- Sinha L N K, Krishna K P and Sinha J K (1970) Sex differences in colour preference of adolescents, *MANAS*, **17**, 17–20.
- Sumner P and Mollon J D (2003) Did primate trichromacy evolve for frugivory or folivory? in Mollon J D, Pokorny J and Knoblauch K (eds), *Normal & Defective Colour Vision*, New York: Oxford University Press.
- Tailby C, Solomon S G, Dhruv N T and Lennie P (2008) Habituation reveals fundamental chromatic mechanisms in striate cortex of macaque, *Journal of Neuroscience*, **28**(5), 1131–1139.
- Teller D Y, Civan A and Bronson-Castain K (2004) Infants' spontaneous color preferences are not due to adult-like brightness variations, *Visual Neuroscience*, **21**, 397–401.
- Valdez P and Mehrabian A (1994) Effects of color on emotions, *Journal of Experimental Psychology: General*, **123**, 394–409.

- Vandewalle G, Schmidt C, Albouy G, Sterpenich V, Darsaud A, *et al.* (2007) Brain responses to violet, blue, and green monochromatic light exposures in humans: prominent role of blue light and the brainstem, *PLoS ONE*, **2**(11), e1247
- Vandewalle G, Schwartz S, Grandjean D, Wuillaume C, Balteau E, Degueldre C, Schabus M, Phillips C, Luxen A, Dijk D J, and Maquet P (2010) Spectral quality of light modulates emotional brain responses in humans, *PNAS*, **107**(45), 19549–19554.
- Viola A U, James L M, Schlangen L J and Dijk D J (2008) Blue-enriched white light in the workplace improves self-reported alertness, performance and sleep quality, *Scand J Work Environ Health*, **34**, 297–306.
- Weiss M R (1997) Innate colour preference and flexible colour learning in the pipevine swallowtail, *Animal Behaviour*, **53**, 1043–1052.
- Wells D L, McDonald C L, Ringland J E (2008) Color preferences in gorillas (Gorilla gorilla gorilla) and chimpanzees (Pan troglodytes), Journal of Comparative Psychology, 122(2), 213–219.
- Wuerger S, Atkinson P and Cropper S (2005) The cone inputs to the unique-hue mechanisms, *Vision Research*, **45**, 3210–3223.
- Zemach I and Teller D Y (2007) Infant color vision: Infants' spontaneous color preferences are well behaved, *Vision Research*, **47**, 1362–1367.
- Zemach I, Chang S and Teller D Y (2007) Infant color vision: prediction of infants' spontaneous color preferences, *Vision Research*, **47**, 1368–1381.