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Abstract

Advances in our understanding of color vision are proceeding on many fronts. These include analyses of the interplay of light and materials in natural scenes, to the genetic, neural, and cognitive processes underlying color sensitivity and percepts. The basic model for color vision, where the light spectrum is first sampled by receptors and then represented in opponent mechanisms, remains a cornerstone of color theory. However, the ways in which these processes are manifest and operate are surprisingly varied and still poorly understood. New developments continue to reveal that color vision involves highly flexible coding schemes that support sophisticated perceptual inferences. Characterizing these processes is providing fundamental insights not only into our experience of color, but into perception and neural coding generally.

Key Terms: color; vision; perception; cognition; constancy; adaptation; neural coding

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Introduction

Color vision has been a focus of interest for centuries, and thus may often appear like a dusty shelf in experimental psychology, filled with principles and debates that were laid to rest long ago. Yet occasionally we are reminded of how little we know. In the spring of 2015 an image of a dress swept across the world because people emphatically differed in whether they saw the stripes as white and gold or blue and black (a discussion that CNN ranked as one of the top talked-about stories of the year). To the public the image provided a striking illustration that a percept as seemingly “simple” as color is not simply given by the stimulus but can instead be subject to widely different interpretations, while among vision scientists it spawned widespread discussion and research over what the basis for those interpretations or inferences might be. It also made it obvious that our understanding of color is not at a point where the explanations could come easily. In fact very many aspects of color vision remain a mystery and the subject of intense activity, and new findings and ideas are constantly emerging that are challenging some of the most basic assumptions about color or are expanding the field in new directions. In this chapter my aim is to highlight some of these developments.

Figure 1. #TheDress image shown in its original color (left) or with the colors inverted (right). People differ in whether they see the original as white-gold or blue-black, but tend to agree on the colors in the inverted image.

Background Issues

In the previous edition of this handbook, Knoblauch provides an elegant and comprehensive introduction to the foundations of color science, and to the background essential to understanding modern color theory. The present chapter builds on this background to illustrate the variety of questions that are currently being asked about our color vision. Other valuable references include the sections on color vision in the New Visual Neurosciences (Chalupa & Werner, 2014), as well as the comprehensive discussion of color vision topics in two forthcoming edited books (Elliott, Fairchild, & Franklin, in press; Luo, in press). Topics in this chapter are focused primarily on psychophysical studies of the mechanisms controlling color sensitivity and appearance, and how these studies are changing our understanding of color. Developments in the physiology of color processing in the retina and cortex are also unfolding at a rapid pace, but in this review are discussed only in relation to these experiments and issues. The chapter also does not cover the active field of colorimetry, which is recently reviewed in (Brainard & Stockman, 2010). An advantage of color science is that many of the processes controlling early sensitivity (e.g. spectral sensitivities of the cones) are known with great precision and consequently allow for precise models and experiments. Tables and descriptions of some of these fundamental resources are available at www.crvl.org (Stockman).

Recent/Emerging Trends

Genes, photopigments, and trichromacy

The vast majority of animal species use vision to sense their world, and in these the capacity for color vision is very common (Jacobs, 2012; Osorio & Vorobyev, 2008). This prevalence speaks to the importance of the visual cues provided by distinguishing differences in the light spectrum. In all known cases the ability to detect spectral information is based on the same principle – sensors that contain photopigments that differ in their absorption spectra. Color vision requires that an organism have at least two different types of receptors with different spectral sensitivities, along with the neural processes to interpret them.

One of the most important insights into human color vision is that in most individuals the ability to discriminate color is essentially three-dimensional or “trichromatic.” This is demonstrated by the observation that the appearance of all spectral stimuli can be matched by different mixtures of just three primaries with fixed spectra, and is why all of the colors on your computer screen are obtained by mixing different light intensities from just red, green and blue primaries. This fundamental limit depends largely on the fact that at most light levels our vision depends on three types of cone photoreceptors with different but overlapping sensitivities to wavelength, and because in each individual receptor the response is “univariant” (i.e. wavelength affects the size of the response but not the form of the response, so that identical responses can occur for a dim light to which the cell is sensitive and to an intense light for which the sensitivity is lower). Univariance dictates that color vision is only possible by comparing the relative responses across receptors with different sensitivities, and thus that the dimensionality of color vision depends on the number of receptor types. This number and the photopigments contained varies widely across species, from animals that have only rod receptors (e.g. cuttlefish, which have colorblind visual systems but nevertheless achieve remarkable camouflage in their skin coloration (Hanlon, 2007)); to rods and a single cone type and thus are again color blind (e.g. including most marine mammals and one primate species, the owl monkey (Jacobs, 2013)); to species that sample the spectrum with a remarkable array of receptor classes (e.g. 12 in the mantis shrimp) (Cronin, Bok, Marshall, & Caldwell, 2014).

In humans with normal color vision the cones contain photopigments that allow them to be maximally sensitive to long, medium, or short wavelengths (L, M, or S) (Smith & Pokorny, 1975; Stockman, MacLeod, & Johnson, 1993) (Figure 2). Individuals with color deficiencies typically lack one of these cone types (and are thus dichromats), or have altered photpigments in which the separation between the L and M sensitivities is reduced (anomalous trichromats) (Neitz & Neitz, 2011). However, even obligate dichromats can exhibit weak trichromacy in large fields or when the pigment density differs across cones, since such factors can introduce effective differences in the spectral sensitivities (Neitz, Neitz, He, & Shevell, 1999).

Figure 2. a) Spectral sensitivities of the L, M, and S cones. b) Arrangements of the receptors measured in the eyes of two observers with adaptive optics (Roorda & Williams, 1999).

While trichromacy remains a cornerstone of our understanding of human color vision, how and why and when it is manifest turns out to be much more complex and intriguing than previously thought. The genes encoding the photopigment opsins were first sequenced in landmark studies by Nathans and colleagues (Nathans, Piantanida, Eddy, Shows, & Hogness, 1986; Nathans, Thomas, & Hogness, 1986). This allowed the photopigments to be characterized and analyzed across individuals or species, and has led to an explosion of new discoveries about the nature and evolution of color vision. For example, the genes for L and M cones are very similar to each other (with sequences that are 98% homologous) and arranged in tandem on the X chromosome, but differ substantially from the S or rod pigment genes which are on autosomal chromosomes (Neitz & Neitz, 2011). These differences have suggested that our trichromatic color vision arose in two stages, the first occurring ~500 mya and based on a dichromatic comparison between S cones and a longer-wavelength pigment, and the second involving a much more recent separation of the L and M cones (~40 mya). These stages have been referred to as the ancient and modern subsystems of our color vision (Mollon, 1989), and are carried by distinct cell types and pathways in the early visual system (e.g. projecting to the parvocellular and koniocellular layers of the lateral geniculate nucleus) (Lee, 2011). Among mammals separate L and M cones and thus trichromacy is limited to primates (Jacobs, 2009). This is the comparison that allows us to distinguish reddish from greenish hues, and an enduring question is what factors drove the evolution of this dimension. For example, the color differences carried by the L vs M cones are ideally positioned to distinguish fruits from foliage as well as the skin tones of conspecifics (Changizi, Zhang, & Shimojo, 2006; Osorio & Vorobyev, 1996; Regan et al., 2001).

More than one receptor type is necessary for color vision, but not sufficient, for the observer must also possess the neural machinery for making the comparisons. A critical question is thus how these post-receptoral mechanisms could have evolved, and genetic studies have revealed some remarkable answers. Trichromacy is routine in old world primates, but very rare among the new world monkeys of Central and South America. In many of these species there is only a single photopigment gene locus on the X chromosome, but with different alleles coding opsins with different sensitivities (Jacobs, 2009). Male new world monkeys thus inherit only one long-wave pigment and are dichromats. Yet because the different alleles occur with high frequency, many females inherit different genes on their two X chromosomes, and through the process of X-chromosome inactivation, the genes from each chromosome are expressed in different receptors. Such females have been shown in behavioral tests to be trichromatic, and thus to distinguish a whole dimension of color vision that is invisible to males (Mollon, Bowmaker, & Jacobs, 1984). The implications of this work for all of neural coding are profound, because it suggests that a complex machinery for interpreting the cone signals does not itself need to be genetically encoded and already in place. Instead, the brain appears able to organize to utilize the information it happens to be given, and this itself raises important questions about how the visual system learns the identity of its inputs (Benson, Manning, & Brainard, 2014).

Polymorphisms also occur in the human cone pigment genes. One involves the substitution of Ser for Ala at site 180 in the pigment molecule with both variants common (~62% Ser). The two versions of the photpigment differ in peak sensitivity by a few nanometers, enough to lead to measurably different behavioral sensitivities (Winderickx et al., 1992). The more extreme spectral shifts resulting in anomalous trichromacy occur in roughly 6% of Caucasian males and are thought to result from unequal crossover in the L and M genes during meiosis (Neitz & Neitz, 2011). Female carriers have the normal gene on one chromosome and the anomalous gene on the other, and thus like new world monkeys have the potential to express both and potentially become tetrachromats (Jordan & Mollon, 1993; Nagy, MacLeod, Heyneman, & Eisner, 1981). Whether this occurs remains uncertain. Female carriers have been reported to make finer partitions when asked to label the visible spectrum (Jameson, Highnote, & Wasserman, 2001), but measurements of color matching and discrimination have in most (but not all) cases found the carriers behave like trichromats (Jordan, Deeb, Bosten, & Mollon, 2010). One possibility is that trichromacy is actually limited postreceptorally (Nagy et al., 1981). For example, the retina also includes rod receptors sensitive to dim light, and at "mesopic" light levels where both rods and cones are active there is again the potential for tetrachromacy. Yet observers remain essentially trichromatic because the rods and cones converge on the same ganglion cells and thus do not retain separate pathways (Lee, 2011).

Recent studies have gone beyond nature's experiments to directly introduce new photopigment genes into organisms. Mice and many other rodents are dichromats but with the S pigment shifted into the ultraviolet, peaking at wavelengths that are invisible to humans (Jacobs, 2009). In transgenic mice with the human L pigment gene inserted, the gene is again expressed creating mice with sensitivity extended to longer wavelengths than ever possible in their ancestors (Jacobs, Williams, Cahill, & Nathans, 2007). Again, this suggests that the visual system is not pre-configured in how it processes the cone signals but instead organizes within the individual for the pigment set they inherit. More remarkably, additional photopigment genes have also been introduced into the eyes of adult new world monkeys (Mancuso et al., 2009). Again, male new world monkeys are born obligate dichromats, but when the third photopigment is introduced it is expressed and they become trichromats over a period of several months. Color discrimination in the treated monkeys approaches the sensitivity of the female trichromats, an improvement which appears far better than observed in transgenic mice. Thus the primate brain seems especially able to take advantage of an added photopigment (Neitz & Neitz, 2014). These findings offers the potential for gene therapies to "cure" color blindness even in adults, and clinical trials for these therapies are currently in the works. It also raises many exciting questions about what the perceptual experience and capacities of these observers will be.

A further big surprise in the story of photopigments and vision has been the recent discovery that the rods and cones are not the only light-sensitive cells in the retina. A small percentage of ganglion cells – the output of the retina – can directly respond to light (Lucas, 2013) (Figure 3). These "intrinsically photosensitivity retinal ganglion cells" (ipRGC's) were revealed as a result of observations showing that humans or mice who lacked photoreceptors nevertheless show some light-specific responses (Schmidt, Chen, & Hattar, 2011). The ipRGC's use melanopsin as the photopigment, and comprise a diverse set of neurons that monitor the overall light level to set "non-image" responses ranging from controlling circadian clocks and sleep to pupil size (Gamlin et al., 2007; Lucas et al., 2014; Spitschan, Jain, Brainard, & Aguirre, 2014). The cells can also combine their intrinsic light responses with inputs from both rods and cones and also project to geniculate pathways (Dacey et al., 2005), potentially supporting conscious percepts such as ambient brightness (Brown et al., 2012). The novel response properties of these cells are leading to a reconsideration of the impacts of artificial lighting (Lucas et al., 2014).

Figure 3. a) Responses and spectral sensitivity of light-sensitive ganglion cells compared to photoreceptors. b) Some the potential light-sensitive functions supported by ipRGC's (Lucas, 2013).

Another critical advance in understanding photoreceptors and color vision has been the application of adaptive optics to studying the retina (Roorda & Duncan, 2015). This technique, borrowed from astronomy, uses a deformable mirror to precisely correct for the optical aberrations of the eye. This allows the cells of the retina to be imaged or stimulated with unprecedented resolution. An early achievement with this technique was to image the cone mosaic within the living eye and to bleach out the different receptor types to reveal the arrangement and relative numbers and of the cones (Roorda & Williams, 1999) (Figure 2). This turns out to be strikingly different even among color-normal observers, with the ratio of L to M cones averaging 2 to 1 but varying from <.5:1 to >16:1 (Hofer, Carroll, Neitz, Neitz, & Williams, 2005). Adaptive optics is also allowing psychophysical studies of color vision to be focused on single cones, by providing the resolution to stimulate with points of light small enough to fall on individual receptors. This has led to asking fundamental questions about what color percepts an individual cone signals, and again the answer is surprising (Brainard, 2015). Specifically, the range of percepts from single cones is far greater than "red, green, and blue," with a variety of other hues as well as achromatic percepts reported (Hofer, Singer, & Williams, 2005). This range suggests that each cone class is not labeled for a specific hue sensation (a result also implied for color percepts in conventional large stimulus fields; (Knoblauch & Shevell, 2001)). The interpretation of a single cone's response may depend on how neighboring receptors are responding and thus on the local spatial distribution of the cones (Brainard, Williams, & Hofer, 2008). While S cones have a fairly regular spatial distribution, the L and M cones are distributed largely randomly, and thus local patches can occur where all the cones are the same, and the visual system may interpret the responses differently when the cone is surrounded by the same cone type or different ones. Analyses of this kind suggest that the visual system makes sophisticated inferences about the information carried even by single receptors. New developments in AO are also on the verge of allowing the same receptor to be targeted and stimulated repeatedly, and will lead to a wealth of studies characterizing the microcircuits for color vision in the retina.

Color opponency and postreceptoral processing

The principles and consequences of trichromacy are central to our understanding of the limits and capacities of color vision and how these depend on the nature of the cone receptors. In the same way, the second pillar of color science - color opponency –remains fundamental to ideas and evidence about how signals from the receptors are recoded and interpreted at subsequent stages of the visual system. Opponency involves comparisons across the cones – e.g. in mechanisms whose activity signals whether the L cones or M cones are more stimulated by a light. This comparison is a logically necessary step to extract information about the spectral characteristics of light independent of the light’s overall intensity, and abundant behavioral and physiological evidence shows that these comparisons are the hallmark of postreceptoral color processing. Yet here again, the basis of color opponency underlying both experience and physiology is proving to be much more complex and varied than expected. In particular, the specific comparisons the visual system makes to represent chromatic information have been surprisingly difficult to unravel. Conventional models of color opponency posit two opponent channels – one signaling red vs. green sensations and the other blue vs. yellow (Hurvich & Jameson, 1957). The stimuli that are perceived as pure red, green, blue, or yellow are thus special because they represent undiluted or “unique” sensations. By this account, other hues, such as orange or purple, instead represent mixtures of the two opponent responses (e.g. red and yellow, or red and blue, respectively). This model was supported by studies suggesting that any hue percept could be described by a mixture of one or two of the unique hue components, while no hues appeared to contain mixtures of the opposing hues (e.g. to appear both red and green at the same time) (Abramov & Gordon, 2005). Thus the model provides a parsimonious account of how observers describe the colors they experience (at least for western English-speaking observers). The problem, however, has been in the quest to identify the mechanisms or factors mediating these judgments. This quest has taken many turns, but these can be roughly grouped into three types of theories that differ in whether the unique hues reflect properties of the observer, the environment, or culture.

Early analyses of color-opponent cells in the primate LGN pointed to a discrepancy between the cells' spectral sensitivities and the response properties predicted by color naming (Devalois, Jacobs, & Abramov, 1964). In particular, short-wavelength lights appear purple and thus contain both red and blue. The redness at short wavelengths suggests that S cones contribute to the red-green channel (and specifically, add with the L cones so that the opponent sensitivity corresponds to L+S-M) (Wooten & Werner, 1979). However, the "red-green" cells instead appeared to difference only the L and M cones, with little S cone input, and this instead predicts that short wavelengths should appear greenish. Such differences were brought to the fore in a highly influential series of studies by Krauskopf and colleagues in the 1980's. They used an adaptation paradigm to desensitize observers to lights that flickered along different axes of color space, and found that the threshold changes were selective for three "cardinal directions" corresponding to luminance (achromatic) contrast, or opponent differences corresponding to L vs. M cone or S vs. L+M cone signals (Krauskopf, Williams, & Heeley, 1982). These cone combinations were subsequently shown to describe the average null points for cells in the lateral geniculate (Derrington, Krauskopf, & Lennie, 1984), and have become a standard stimulus framework for specifying colors (in spaces where the axes correspond to the cardinal dimensions) and for exploring post-receptoral color coding (Derrington et al., 1984; MacLeod & Boynton, 1979). As noted, the cardinal axes are not aligned with the unique hue axes (Krauskopf et al., 1982; Webster, Miyahara, Malkoc, & Raker, 2000; Wuerger, Atkinson, & Cropper, 2005). Specifically, the L vs. M axis is a color variation that observers on average describe as red vs. blue-green, while the S axis varies in appearance from purple to yellow-green. Conversely, the stimuli that appear pure blue, yellow, or green all lie along diagonals within the cone-opponent space, and thus do not isolate the responses of either of the cardinal mechanisms. (Despite this, the axes are often labeled for convenience as red-green or blue-yellow. However, this shorthand underplays the marked discrepancies between the cardinal and classical opponent channels. For example, hue scaling studies have shown that the two poles of the S axis correspond on average to equal amounts of red and blue (+S) or equal amounts of yellow and green (-S) (Malkoc, Kay, & Webster, 2005). Thus in terms of its appearance it is as accurate to describe the S axis as "red-green.")

Figure 4. a) conventional 2-stage model of color vision where the signals from the receptors are combined to form opponent (chromatic) or non-opponent (luminance) channels. b) spectral sensitivities of the opponent channels and the wavelengths corresponding to sensitivity nulls or unique hues. c) A cone-opponent color space defined by variations in LvsM cone activity or SvsLM activity at constant luminance. Labels show the average directions of the unique hues.

The mismatch between the cardinal axes and unique hues raised questions that continue to be widely asked but yet to be firmly answered – what is the basis for the unique hues, and are they actually unique? One approach to this question has sought to explore color coding at subsequent stages of the visual system. Information about color may be represented in different ways at different stages of the visual pathway, and thus a representation corresponding to the phenomenal opponent axes may emerge only later in the visual stream. For example, some models posit that the geniculate axes could be rotated in the cortex to create mechanisms with the spectral sensitivities consistent with color naming (De Valois & De Valois, 1993). The required transformations are not found in the earliest visual cortical stage (V1), even though a stronger bias may emerge for cells tuned to blue and yellow (Lafer-Sousa, Liu, Lafer-Sousa, Wiest, & Conway, 2012). On the other hand, cells in posterior inferotemporal cortex have been reported to show clustering of their tuning around the unique hues (Stoughton & Conway, 2008), though this result may be confounded with differences in the saturation of the stimuli (Mollon, 2009). A remapping of color organization has also been suggested by analyzing fMRI responses to color. For example, Brouwer and Heeger found that BOLD responses in V4 and V01 but not V1 or other early visual areas showed a pattern consistent with the perceptual organization of color (Brouwer & Heeger, 2009). Finally, there is also some behavioral evidence for mechanisms with sensitivities tied to the unique hues. Mollon and Danilova found that color discrimination is selectively enhanced for stimuli demarcated by a blue-yellow axis (Danilova & Mollon, 2011). Such results are important because they reveal an objective sensitivity correlate of subjective appearance. Yet again, it is not clear that such mechanisms are uniquely tuned for the phenomenal unique hues (Danilova & Mollon, 2014).

A second approach has been to reanalyze how the cone signals are combined early in the visual system. The receptors are burdened with supporting all of vision, and not simply color, and many of the postreceptoral pathways they feed into may not be used for color appearance, even if they have cone opponency (which as discussed below, may be equally important for representing spatial information, such as the borders or edges defined by color differences). If, like the photosensitive ganglion cells, the pathway conveying color percepts were only a small fraction of the retinal output, then it may have been overlooked. This idea has recently been proposed by Schmidt et al., who suggested that the S cones do feed into a subset of retinal ganglion cells to add to either the L cone or M cone signals (Schmidt, Neitz, & Neitz, 2014). This changes their spectral sensitivity from L-M to L-M+S or L-M-S, and thus to sensitivities that are closer to the cone combinations predicted by color appearance. That is, cells that directly signal red-green and blue-yellow sensations might already be built very early in the retina.

Importantly, both of these accounts presuppose that the unique hues really are special, and thus that the problem is to find the neural architecture where their representation becomes explicit. However, an alternative is that they do not reflect a pure neural signal, and that red and yellow are no more primary than orange. In fact recent studies have questioned whether the unique hues are more fundamental, by showing that they behave similarly to non-unique hues on different tasks (Bosten & Boehm, 2014; Bosten & Lawrance-Owen, 2014; Malkoc et al., 2005; Wool et al., 2015). Physiologically, the spectral sensitivities of cells in primary visual cortex do not show the clear clustering into discrete cone-opponent combinations found in the retina and LGN (Gegenfurtner, 2003; Lennie & Movshon, 2005; Solomon & Lennie, 2007). Instead, the cardinal axes appear to be recombined to give rise to "higher-order" color mechanisms that each tuned to a different direction in color space, and may show a columnar organization in terms of hue selectivity (Xiao, Wang, & Felleman, 2003). The responses also become more narrowly-tuned or selective for the range of colors they respond to (De Valois, Cottaris, Elfar, Mahon, & Wilson, 2000; Kiper, Fenstemaker, & Gegenfurtner, 1997). Part of this transformation may reflect nonlinearities in cortical processing (Horwitz & Hass, 2012). However, a wide range of physiological and psychophysical evidence suggests that the visual system can be selectively sensitive to hues or color-luminance combinations that are intermediate to the cardinal axes. For example, performance in tasks like visual search or masking, or in how colors interact in apparent motion cannot be predicted from the separable chromatic signals along the cardinal axes (Eskew, 2009). Similarly, when observers are adapted to a field that is modulated in color along one axis in color space, the sensitivity losses are specific to the adapting hue angle, and this selectivity occurs whether the modulation is along the cardinal axes or intermediate axes (Krauskopf, Williams, Mandler, & Brown, 1986; Webster & Mollon, 1994). These results point to a "multiple channel" representation of color in the same way that adaptation to orientations or spatial frequencies revealed multiple channels in spatial vision (Graham, 1989). Moreover, this adaptation strongly affects the perceived hue and saturation of stimuli, and thus must be affecting mechanisms that are directly involved in color appearance (Webster & Mollon, 1994). The implication is that color might be encoded in ways that closely parallel other stimulus dimensions such as spatial orientation – by the distribution of activity across multiple mechanisms that sample the dimension with channels tuned to different but overlapping ranges of the stimulus. Such models pose a challenge for the concept of unique hues, because the underlying neural responses are not unique. That is, within the population of channels, a stimulus that appears "pure red" is represented by a distribution of responses in the same way as orange or purple. An advantage of this coding scheme is that different hues can be represented explicitly, by which channel is most active, rather than implicitly, by the relative activity in underlying cardinal or unique hue mechanisms (Zaidi, Marshall, Thoen, & Conway, 2014). (Again, this is very similar to the ways in which orientation is thought to be encoded, by many cells each tuned to a different angle, rather than by the relative responses in cells that only prefer horizontal or vertical.) Such population codes could also allow color to be represented by vector averaging in ways analogous to how motor commands are controlled (Wachtler, Sejnowski, & Albright, 2003).

Similar stimulus selectivity also occurs for combinations of luminance and color. For example, masking or adaptation to a "bright red" produces a selective sensitivity change that cannot be accounted for by the separate "bright" or "red" components of the stimulus (Gegenfurtner & Kiper, 1992; Webster & Mollon, 1993). Thus even pure "light" and "dark," the third axis of conventional opponent theory, do not appear to be represented by pure achromatic mechanisms. This is also consistent with the responses of geniculate and cortical cells within putative color pathways, which are often sensitive to different combinations of luminance and chromatic contrast (Derrington et al., 1984; Horwitz, Chichilnisky, & Albright, 2005).

A further revision of conventional opponency is that the opponent dimensions themselves may be represented by separate pairs of "monopolar" mechanisms. That is, red and green may be encoded separately rather than yoked as opposite responses within a common channel. There are several arguments for this separation. First, red-green or blue-yellow are not in general complementary (i.e. they do not mix to produce gray), and this means that they do not correspond to complementary or opposite weightings of the cone signals (Webster et al., 2000; Wuerger et al., 2005) (Figure 4). For example, the complement of red is cyan, while for green it is a reddish purple. Moreover, across observers the unique hues are uncorrelated – so that knowing someone's null for red does not predict their choice for green (Kuehni, 2004; Webster et al., 2000). Separate monopolar mechanisms are also suggested by studies showing that the opposing color pairs can be independently adapted (Beer & MacLeod, 2000; Krauskopf et al., 1982), and that they show differences in spectral tuning (De Valois, De Valois, Switkes, & Mahon, 1997) and in how perceived saturation scales with field size (Abramov, Gordon, & Chan, 1991). Distinct on and off pathway are also well established for luminance increments and decrements, and have recently been shown to underlie a number of perceptual differences (Kremkow et al., 2014). Finally, color percepts may also differ for bright and dark colors in ways suggestive of separate mechanisms. A curiosity of unique yellow is that yellow itself only exists as a light color, in luminance increments. When the chromaticity is instead shown as a decrement it appears brown, and unique brown turns out to require a different balance of cone signals than unique yellow (Buck, 2015).

There may be several advantages for splitting opponent mechanisms in two. First, cortical cells have low spontaneous activity, and thus can only modulate their responses by excitation. The +L/-M and +M/-L opponent responses within the lateral geniculate may therefore be rectified to carry opponent signals but now as two separate excitatory responses (De Valois & De Valois, 1993). Notably, because they are no longer yoked, at this stage it is possible to contrive stimuli that appear both red and green at the same time, e.g. by stabilizing a red-green edge so that one color fills-in to the other (Crane & Piantanida, 1983). A second proposed advantage is that splitting the axis in two improves the signal to noise ratio while preserving an efficient representation of color (MacLeod, 2003).

Thus to summarize, it has not been possible to settle the link between the neural coding of color and the phenomenal appearance of color as embodied in Hering's opponent process theory. Cells with sensitivities predicted by the unique hues have not yet been found, nor is it evident that these hues represent nulls or otherwise unique neural responses. Further, it remains unclear which subpopulations of cells are involved in mediating color appearance.

What of the final unique stimulus – gray? This also reflects a null point in most models of color vision and is specifically the null of all three opponent mechanisms. As such it is the stimulus that anchors all of color space (since any other stimulus may be encoded by how it differs from gray). Deviations from gray correspond to contrast, and a standard assumption is that contrast is represented by the intensity of the response rather than which neuron responds. However, there is at least the possibility that different contrast ranges recruit different populations of cells (Albrecht & Hamilton, 1982; MacLeod, 2003; Webster & Wilson, 2000), and thus that contrast is also represented partly by a population code. On the other hand, gray is a case where a direct link can be made between appearance and sensitivity. Webster and Leonard showed that the stimulus that appears gray to an observer is close to the stimulus that does not produce a color afterimage (Webster & Leonard, 2008). Thus the stimulus that appears phenomenally neutral is also one that does not alter the relative sensitivity of chromatic mechanisms, suggesting that the neutral experience of gray does reflects an actual sensitivity null or balance within the neural mechanisms encoding color.

Color and cognition

Regardless of whether or not the unique hues have a distinct neural substrate, this leaves the question of why they appear to be more fundamental or pure sensations. An alternative answer is that the unique hues are not built into the structure of the brain but instead reflect the structure of the world. That is, the unique hues may look special because they correspond to special properties of the color environment. For example, unique blue and yellow fall very close to the daylight locus of natural variations in lighting (Mollon, 2006). Similarly, pure red may correspond to a salient stimulus such as blood or ripening fruit. By this account, there is no necessary relationship between neural responses and sensations, for we simply may learn which pattern of responses are more diagnostic about the world, and what constitutes a primary hue may be more a question of criterion than sensitivity (Mollon & Jordan, 1997). On the other hand, the different explanations for color appearance may be intimately linked. For example, a mechanism could be tuned to blue-yellow specifically because this is a principal dimension of variation in the color environment (Lee, 1990; Shepard, 1992), and thus the most efficient coding to represent the environment (Lee, Wachtler, & Sejnowski, 2002; Ruderman, Cronin, & Chiao, 1998; Webster & Mollon, 1997).

Whether color percepts are learned relates to the broader question of "cognitive penetrance," or the extent to which sensory signals could be shaped by top-down influences or other cognitive processes. There are arguments that percepts must necessarily be learned, for the visual system must represent the same world through very different sensory signals (O'Regan & Noe, 2001). For instance, color appearance remains largely constant between the fovea and periphery, even though spectral sensitivity and neural processing is very different at the two loci. Models of color vision, and perception more generally, have also been advanced based purely on learning the statistical structure of the world such as the joint probability distributions of different spectral stimuli (Long, Yang, & Purves, 2006). This learning is also fundamental to many applications of Bayesian inference for estimating the stimulus prior. There are a number of intriguing examples of knowledge and experience shaping our color percepts. For example, Hansen et al. found that grayscale images of familiar objects (e.g. a banana) appeared distinctly tinted (e.g. yellow) and thus that complementary tints had to be added to the images to null these biases (Hansen, Olkkonen, Walter, & Gegenfurtner, 2006). A second recent example is in color synaesthetes, who report that numbers or letters appear in different hues. These cross-modal associations reflect actual percepts, and the propensity to experience them is a heritable trait. However, the specific color-grapheme associations may be learned. Witthoft and Winawer studied several synaesthetes who all had similar color-letter pairings, and who all turned out to have had the same colored alphabet toy as children (Witthoft & Winawer, 2013). Finally, learning has also been argued to play a major role in color preferences and in cross-modal associations involving color (Palmer, Schloss, & Sammartino, 2013).

Studies of visual attention have found that attention can modulate visual appearance including perceived contrast (Carrasco, Ling, & Read, 2004). The perceived lightness of an object can also be affected by which features or regions of the object are attended to (Toscani, Valsecchi, & Gegenfurtner, 2013). Both color perception and color memory have been widely studied, but largely as separate and independent processes (Allred & Flombaum, 2014). However, recent evidence points to important interactions between them. For example, scenes with color are more easily remembered (Gegenfurtner & Rieger, 2000). Conversely, as noted above long-term memories can bias color appearance (Hansen et al., 2006), and working memory can also impact percepts. For example, Olkonnen and Allred found the contextual effects in color perception are reduced when a short delay is introduced between the stimuli to be compared, and suggested that this resulted because the delay allowed a perceptual prior to more strongly influence the judgment (Olkkonen & Allred, 2014). Such interactions between color percepts and attention and memory are consistent with findings that attentional and working memory traces are seen within early primary visual cortex (Gandhi, Heeger, & Boynton, 1999; Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009).

Most studies of color and cognition have focused on the relationship between language and color. Are the unique hues or other basic colors similar to how all humans experience color, or defined arbitrarily by how a culture chooses to divide the spectrum? Berlin and Kay's World Color Survey established that there are strong correspondences in the color categories of different languages, pointing to strong universal tendencies in color naming and arguing against the prevailing theories of linguistic relativity (Kay, Berlin, Maffi, Merrifield, & Cook, 2009). However, this issue has seen a resurgence of interest (Kay & Regier, 2006). Recent studies have mustered support both for and against common categories across languages (Figure 5). For example, statistical analyses of data from the World Color Survey reveal that the focal stimuli for basic color terms across different languages are much more similar than could be expected by chance (Lindsey & Brown, 2006; Regier, Kay, & Cook, 2005). Conversely, Roberson et al. revisited early work suggesting that languages with few color terms nevertheless tend to show perceptual or memory biases consistent with the color divisions in languages with more terms. However, they found that the errors were more readily predicted by the categories specific to the language (Roberson, Davidoff, Davies, & Shapiro, 2005). Understanding such effects is further complicated by the fact that linguistic differences and similarities covary with other factors such as environmental differences. For example, many languages lack separate terms for green and blue, and Lindsey and Brown noted that these tended to occur in regions with high UV exposure that might render individuals less sensitive to shorter wavelengths (Lindsey & Brown, 2002) (though this alone is unlikely to account for their color naming behavior; (Hardy, Frederick, Kay, & Werner, 2005)).

Figure 5. a) A Munsell hue palette commonly used to test color naming. Color labels for the palette in English (b) or Berinmo (c). d) Distribution of color naming across the languages of the World Color Survey.

A further common approach to this question has been to test for categorical effects in perception or memory; e.g. to test whether two stimuli are more easy to discriminate or recall when they fall in different verbal categories (e.g. blue and green) than when they fall within the same category (two shades of blue). Gilbert et al. used a visual search task and found that observers were faster at detecting a green target among blue distractors (or vice versa), than when targets and distractors were both shades of blue or green but matched for an equivalent hue difference (Gilbert, Regier, Kay, & Ivry, 2006). Similarly, Winawer et al. found that speakers of Russian, which has separate color terms for light and dark blue, were faster at discriminating these hues than English speakers, which instead label the stimuli with the same color term (Winawer et al., 2007). These effects are disrupted by a verbal interference task (Roberson & Davidoff, 2000) and can be lateralized to the left hemisphere (Gilbert et al., 2006), consistent with an effect of language. Moreover a number of studies have found evidence for categorical color coding in neural responses (Brouwer & Heeger, 2013; Clifford et al., 2012; Zhou et al., 2010). They have also been found in tasks that require memorizing colors or judging their similarities (Kay & Kempton, 1984; Pilling, Wiggett, Ozgen, & Davies, 2003). However, the nature of these categorical effects remains unclear. Infants show categorical color coding but the lateralization is different than adults (Franklin et al., 2008); and both the lateralization and the categorical effect itself have not always replicated (Brown, Lindsey, & Guckes, 2011; Witzel & Gegenfurtner, 2011). Moreover, it is uncertain whether the effects reflect an influence of language at the level of the percept or the response. For example, within-category responses could be impeded if two stimuli were visibly “different” but fell within the “same” verbal category, analogous to Stroop interference. When categorical effects were tested in a perceptual grouping task, in which a speeded response was not required, there was little evidence for a bias (Webster & Kay, 2012).

When interpreting these studies, it is important to note that even when categorical effects are found, their impact tends to be small. Clearly, we do not experience the spectrum in terms of a few discrete hue bands, and thus these potential top down effects at best only weakly modulate our percepts. Moreover, when interpreting color naming, it is also important to recognize that the variability among speakers within a language is often far greater than the differences across languages. The stimuli selected as unique hues show enormous individual differences (Kuehni, 2004; Webster et al., 2000). For example, unique green spans a large portion of the visible spectrum (Welbourne, Thompson, Wade, & Morland, 2013) (Figure 6). Malkoc, Kay, and Webster also found that hue angles chosen for unique and binary hues reliably varied enough that the categories overlapped (Malkoc et al., 2005). Thus what one person described as unique yellow another might choose as the best example of orange. Moreover, the selections for different hues were again uncorrelated even for nearby hues, so that someone’s choice for orange could not be predicted from the hues they selected for the supposed red and yellow component colors. Striking individual differences also occur in the World Color Survey (Webster & Kay, 2007). Lindsey and Brown found that respondents from different languages were often more similar in how they named the palette colors than individuals from the same language, and that this reflected different patterns or naming “motifs” that repeated across many languages (Lindsey & Brown, 2009). Recently these differences were examined among the Hadza, a hunter-gatherer society in Tanzania (Lindsey, Brown, Brainard, & Apicella, 2015). Hadza has only three consensus color terms (white, black, and red). Responses across individuals vary widely and for many samples individuals may not choose a term. However, across speakers many of the basic terms in languages like English are used, so that the characteristic evolutionary trajectory of the color lexicon is already present in the population before being acquired by the individual.

Figure 6. Variability in color appearance. Points plot the directions of stimuli chosen for unique or binary hues by a large sample of color-normal observers.

The reasons for these large individual differences remain very obscure. As we discuss below, they cannot be accounted for by individual differences in the spectral sensitivity of the observers, because even individuals with very large sensitivity differences can select very similar unique hues (Brainard et al., 2000; Miyahara, Pokorny, Smith, Baron, & Baron, 1998), and also because most peripheral sensitivity differences predict correlated variations in the hues which as noted are not found (Webster et al., 2000). One possibility is that color categories themselves do not need to be precisely co-registered across individuals in order for people to communicate effectively about color (Komarova & Jameson, 2008; Steels & Belpaeme, 2005; Webster & Kay, 2007). But whatever their basis, this inter-observer variability is a prominent feature of color perception and one that will likely be important for ultimately understanding the basis for the experience and language of color.

Contextual effects on color appearance

In normal viewing colors are always experienced as part of a scene, rather than as isolated patches. The surrounding context – in both space and time – has enormous influences on color appearance. This has long been recognized in the distinction between aperture colors (uniform fields viewed on a black background) and surface colors (stimuli perceived as part of a context). All aperture colors appear bright, and thus can never give rise to percepts like black, gray, or brown, which depend on induction from brighter surrounds (Cicerone, Volbrecht, Donnelly, & Werner, 1986; Fuld, Werner, & Wooten, 1983). As more information about the scene is added, the visual experience of color also increases from simple attributes (hue, saturation, and brightness), to percepts that come closer to the actual viewing geometry (e.g. of lightness or reflectance, shading, and transparency). The processes through which surrounds influence appearance are complex and still poorly understood. However, it is clear that these engage multiple mechanisms and levels of analysis (Shevell, 2012; Shevell & Kingdom, 2008) (Figure 7). Consequently, the effects of a complex field cannot in general be reduced to an equivalent uniform surround color. Surrounds can alter not only the average color but also the perceived variance or saturation of a test stimulus (Brown & MacLeod, 1997; Singer & D'Zmura, 1994; Webster, Malkoc, Bilson, & Webster, 2002). The effects can also be strongly biased by inferences about objects and lighting (Bloj, Kersten, & Hurlbert, 1999). Moreover, even with uniform surrounds the influence can vary in ways that are difficult to reconcile with simple coding schemes. For example, Ekroll et al. have shown that chromatic contrast effects are relative to the background inducing color and thus inconsistent with a single "gray" norm in the representation (Ekroll, Faul, Niederee, & Richter, 2002).

Figure 7. Examples of spatial context effects in color. a) the two words are displayed with the same physical chromaticity but appear very different because of induction from the intervening chromaticities (Monnier & Shevell, 2003). b) Edge colors tend to spread into intervening areas in the water color illusion (Pinna, Werner, & Spillmann, 2003).

A contextual effect that has received intense scrutiny is the phenomenon of "color constancy" (Foster, 2011). Color constancy refers to the problem of how the visual system disambiguates the color of surfaces and illuminants – i.e. how we can distinguish a red object in white light from a gray object in red light. This is not possible by considering a single surface in isolation, because the light reaching the eye confounds information about the illuminant and the surface reflectance (Figure 8). That is, the same spectrum could result from a longwave reflectance under a broadband light or a uniform reflectance under a longwave light. However, a great deal of work has pointed to the stimulus conditions that could support constancy, as well as the degree to which humans can actually achieve it. One crucial insight is that color constancy must involve comparing the cone signals from different locations or points in time. In the original retinex models of Land and McCann, constancy was achieved by normalizing the average responses within each class of cones (Land & McCann, 1971). This tends to compensate for a change in illumination by rescaling the cones so that "gray" corresponds to the average color in the scene, a process effectively similar to cone-specific gain changes in the cone sensitivities (known as von Kries adaptation) (Brainard & Wandell, 1992). For example, shifting the light to longer wavelengths increases the relative L cone capture, and this imbalance can be restored by reducing the L cone sensitivity.

Figure 8. A Munsell palette under two light sources, illustrating the problem of color constancy of unconfounding the color of surfaces and lighting (Shevell & Kingdom, 2008).

A second important advance involved computational analyses of physical spectra and the degree to which the visual system could in theory recover the surface color. This work has shown that natural reflectance and illuminance functions do not vary arbitrarily with wavelength and instead change gradually across the spectrum. As a result most of the differences between spectra can be captured by a low-dimensional model with as few as three basis functions (Cohen, 1964; Judd, MacAdam, & Wyszecki, 1964). This is important because a trichromatic visual system provides only a three-dimensional estimate of the stimulus spectrum, and implies that this coarse sampling is adequate to represent natural spectra (Dannemiller, 1992; Maloney, 1986). Analyses of this kind have also revealed the limits of constancy mechanisms. For instance, von Kries scaling cannot completely discount an illuminant change because the relative cone signals depend on the reflectance spectrum, and will produce the wrong answer when the average reflectance in the scene is not gray (Worthey & Brill, 1986). Thus additional mechanisms beyond the receptors are required. Some of these may involve mechanisms sensitive to higher-order statistics beyond the mean chromaticity (e.g. the correlations between luminance and chromaticity can distinguish between a red room in white light and white room in red light) (Golz & MacLeod, 2002). Others may involve Bayesian inferences about the spectral characteristics of natural scenes, which can provide a prior for choosing between different interpretations of the cone excitations (Brainard et al., 2006). Still others have been implicated in how we perceive color in naturalistic settings where there can be multiple sources of lighting and diverse types of surfaces (Maloney, 2002).

Finally, a third advance was recognition that the degree of constancy depends on the task the observer is required to perform. Arend and Reeves showed that subjects exhibit greater constancy when asked to compare whether two surfaces “were cut from the same cloth” than when required to directly match the colors (Arend & Reeves, 1986). Similarly, subjects are generally very good at detecting whether changes in a palette of stimuli correspond to a change in illumination (in which there is roughly a common shift in all the spectra) versus a change in reflectance (in which there are non-uniform changes in the palette elements) (Foster & Nascimento, 1994). Such results point again to a wide variety of mechanisms supporting different aspects of constancy, and have led to a profusion of studies exploring different cues and processes and how these are combined (Foster, 2011; Smithson, 2005). Humans do not show perfect constancy, but generally improve the more cues are provided about the surfaces and lighting and the more the judgments are about the inferred surfaces in the scene rather than their actual color appearance.

Color constancy is often described as discounting the illuminant, but as the preceding suggests, this does not mean that the illuminant is not also perceived. We can readily detect changes in lighting owing to shading and shadows, while still perceiving the underlying surface properties. Many striking illusions have shown the power of these lighting and transparency effects on perceived lightness and color (Adelson, 1993; Lotto & Purves, 1999). This suggests the intriguing possibility that we directly represent both the lighting and the surface at each point in the scene, as distinct layered percepts (Anderson & Winawer, 2005) (Figure 9).

The perception of a transparent layer again involves sophisticated inferences and sensitivity for physical properties of the world including the ordinal relationships between light intensities on different sides of a border and the gradients defining the border (Kingdom, 2008). When the stimulus violates these assumptions then a region perceived as shadow can convincingly switch to paint.

Figure 9. Percepts of lighting and surfaces. a) The chess pieces are identical but their lightness depends on how the image is parsed into the object or intervening fog (Anderson & Winawer, 2005). b) Shadows are normally discounted from the appearance of surfaces, but can appear as part of the surface when the image violates assumptions about shading.

Many of these ideas and illusions were brought to the fore to try to account for the appearance of the dress image. The lighting in the image is ambiguous, and a standard explanation for the different percepts was whether the individual perceived the dress itself as backlit and thus in shadow (so that the light stripes appear as white cloth in bluish shade), or directly lit (so that the stripes were instead blue cloth illuminated by white light) (Brainard & Hurlbert, 2015). What remains unclear is why different people see it different ways, and why it is so hard to switch between the percepts in the way that one can for other ambiguous illusions like a face versus vase or Necker cube. At the time of this writing there is a frenzy of research to understand the phenomenon, and thus the answers may soon be at hand. However, the first round of reports suggests that these answers will again be complex and will likely involve many factors (Gegenfurtner, Bloj, & Toscani, 2015; Lafer-Sousa, Hermann, & Conway, 2015; Winkler, Spillmann, Werner, & Webster, 2015). One initial finding is that different percepts are very specific to the bluish tints in the image, for the differences disappear when the colors are inverted or rotated to other hues. This has been attributed to inferences about the color-luminance relationships expected in natural lighting and shading. For example, the lighting within shadows tends to be from indirect sky and thus bluer, and the visual system may have a greater tendency to discount this blueness from the surface than other hues.

Calibrating color vision

As the foregoing suggests, color constancy is usually framed in the context of discounting extraneous changes in the proximal stimulus such as the lighting. However, an equally important aspect of constancy involves compensating for changes in the observer. The optical and neural properties of the visual system undergo dramatic changes during normal development and aging, or when the system is compromised by disease. Moreover, there are enormous variations in sensitivity and processing across the visual field. Despite this, percepts often appear relatively stable as we age, or between the fovea and periphery. This perceptual constancy is again supported by a variety of mechanisms that serve to discount our sensitivity limits from our percepts.

A clear example of these compensations is the perception of white. The crystalline lens of the eye contains a pigment that selectively absorbs shortwave light, shielding the retina from the damaging effects of exposure to ultraviolet radiation (Figure 10). The lens pigment density steadily increases as we age, and thus increasingly less shortwave light reaches the receptors (Pokorny, Smith, & Lutze, 1987). In an average 70 year old this amounts 25 times less light at 400 nm compared to an infant eye. Yet judgments of the spectrum that appears achromatic changes very little with aging (Werner & Schefrin, 1993). Similarly, the central fovea is screened by macular pigment which again selectively filters short wavelengths. The density of the pigment varies with factors such as diet, and declines rapidly with eccentricity so that there is little macular pigment screening beyond a few degrees (Hammond, Wooten, & Snodderly, 1997). Thus the receptors surrounding the fovea receive much more shortwave light, yet again the stimulus that appears white remains very constant between the fovea and periphery (Webster & Leonard, 2008). This suggests that each site on the retina is locally calibrated for the average incident light level.

Figure 10. a) The human lens at different ages showing the progressive increase in pigment density. b) Simulations of how an image would appear to a young observer (left) or older observer without (middle) or with (right) compensation for their reduced spectral sensitivity (Webster, Juricevic, & McDermott, 2010).

The calibration for gray could be achieved by cone-specific (von Kries) adaptation, in the same way that this adaptation can factor out the average change in cone responses from an illuminant change. Studies of chromatic adaptation in the fovea and periphery are consistent with a very early and potentially receptoral site for the compensation (Webster & Leonard, 2008). However, an important difference is that the compensation for the observer sensitivity must include adaptation with a longer time constant, because it survives an intervening period of dark adaptation (and thus the fovea and periphery are not simply under adaptation to the same current stimulus). There is now substantial evidence for color adaptation effects operating over multiple timescales (Webster, 2015). For example, wearing tinted contact lenses or exposing observers to spectrally-biased lighting for several hours produces changes in color percepts that are also long lasting (Belmore & Shevell, 2008; Eisner & Enoch, 1982; Neitz, Carroll, Yamauchi, Neitz, & Williams, 2002). Very persistent color aftereffects also occur in patients following cataract surgery (Delahunt, Webster, Ma, & Werner, 2004). The replacement of their lens floods their retina with short wavelength light, and it can take weeks of months for their white settings to readapt to this change. This suggests the possibility that the calibrations for color vision and other perceptual attributes might track the timescales of change in the stimulus. However, the sites and mechanisms controlling even a simple stimulus change like an increase in lens pigment remain poorly understood (Tregillus, Werner, & Webster, in press). The timescales of calibrations also blur the distinction between adaptation-induced sensitivity changes and learning. The McCollough effect is a classic and highly-investigated effect in which color aftereffects are contingent on the orientation of adapting color bars (McCollough-Howard & Webster, 2011). One component of the aftereffect is essentially permanent – lasting until it is extinguished by exposing the observer to the opposite pairing of color and orientation (Vul, Krizay, & MacLeod, 2008).

Similar processes have been postulated to calibrate the perception of hue. For example, a prominent account of unique yellow is that it reflects a normalization of the relative responses in the L and M cones for the average spectral stimulus we are exposed to (Pokorny & Smith, 1977). (Unique yellow is at a wavelength of about 570 nm, and thus does not stimulate the S cones. However, more generally, this calibration must also adjust for desaturated yellows including gray, and thus also requires balancing the weights of all three cone classes.) This adjustment can potentially account for the fact that unique yellow is largely unaffected by the enormous individual differences in cone ratios (Brainard et al., 2000). In fact, it is difficult to find associations between variations in color appearance and any spectral sensitivity differences, though some recent studies have reported a relationship between unique green and the L:M cone ratios (Schmidt et al., 2014) or macular pigment density (Welbourne et al., 2013). In general however, one of the most striking features of the large normal variations in color appearance is that they are largely independent of the pronounced differences between observers in their sensitivity (Webster et al., 2000).

As we noted, cone-specific adaptation can provide complete constancy for gray (since the cone responses are equated across the two contexts for the average stimulus change), but leaves residual errors in the cone responses to other spectra (since each spectrum introduces somewhat different changes in the cone ratios). However, color appearance settings across age or between the fovea and periphery show less variation than predicted by the differences in lens and macular pigment (Bompas, Powell, & Sumner, 2013; O'Neil & Webster, 2014; Webster, Halen, Meyers, Winkler, & Werner, 2010). This suggests higher-order adjustments beyond the cones. Some of these adjustments may be surprisingly sophisticated. For example, the Abney effect is a classic phenomenon of color vision in which the perceived hue of a wavelength changes when desaturated by adding a white light (Burns, Elsner, Pokorny, & Smith, 1984). This interaction has been attributed to nonlinearities in color coding, with little functional utility. However, recent studies instead suggest that it may again reflect mechanisms that adapt color vision to discount the observer’s sensitivity. Mizokami et al found that the Abney effect does not occur when the stimulus is instead a Gaussian spectrum desaturated by increasing its bandwidth (Mizokami, Werner, Crognale, & Webster, 2006; O'Neil et al., 2012). They argued from this that the visual system might assume a Gaussian profile for the stimulus spectrum and compensate for the bandpass filtering of the cones in order to maintain constant hue percepts, e.g. tied to the estimated peak wavelength of the Gaussian. By this account, the traditional Abney effect occurs because the visual system is applying the correct compensation for natural spectra to a spectrum which is unnatural.

Despite these adjustments, there are clearly limits to how well the visual system can stabilize color appearance. For example, some hue differences remain between the fovea and near periphery, and color vision does vary with eccentricity as chromatic sensitivity declines (McKeefry, Murray, & Parry, 2007; Mullen & Kingdom, 2002; Parry, Panorgias, McKeefry, & Murray, 2012). Moreover, color deficient observers with greatly reduced sensitivities do differ in percepts such as color salience or their unique hues (Boehm, MacLeod, & Bosten, 2014; Neitz et al., 2002). However, these changes are often far smaller than predicted by the threshold sensitivity changes. This provides an important caveat for inferring chromatic mechanisms from visual percepts. Many studies of color vision have sought to define the underlying physiology or anatomy from behavioral measures of sensitivity or appearance. However, the system itself is designed to remove as far as possible these sensitivity limits from the representation of color.

Color vision must be compensated not only for individual colors but also for the gamut of colors. These adjustments may again occur over a range of timescales. Short-term exposure to variations in chromaticity (chromatic contrast) results in selective losses in sensitivity to the chromatic directions of the variation (Webster & Mollon, 1994). We noted earlier that the selectivity of these effects for different chromatic axes is one source of evidence for multiple higher-order color channels in visual cortex, where the sensitivity changes are thought to occur (Krauskopf et al., 1986). Several recent studies have demonstrated separate longer-term adaptation to luminance contrast, e.g. so that several hours of exposure to low contrast environments increases sensitivity to contrast (Kwon, Legge, Fang, Cheong, & He, 2009). Whether there are parallel longer-term effects for color have yet to be established (Tregillus & Webster, 2014). However, some form of very long-term adaptation to contrast is required to account for the relative scaling of luminance and chromatic contrast. Because the cone sensitivities overlap, the opponent signal for color (e.g. L-M) is necessarily much smaller than the non-opponent signals coding luminance (L+M) (MacLeod, 2003). However, sensitivity to chromatic stimuli is correspondingly higher (Chaparro, Stromeyer, Huang, Kronauer, & Eskew, 1993), and subjectively the world does not appear to vary less in color than it does in brightness (McDermott & Webster, 2012a). This could occur if postreceptoral mechanisms normalize their sensitivity for the range of their inputs. These ideas have also been applied to understanding color percepts in anomalous trichromats. Again these individuals have two closely similar longwave pigments, and thus greatly reduced range of difference signals provided by comparing these cones. Yet many anomalous observers show greater sensitivity and can judge reddish-greenish hues to be more salient than their photopigments predict (Boehm et al., 2014; Regan & Mollon, 1997; Webster, Juricevic, et al., 2010).

The foregoing suggests that adaptations of different forms play a fundamental role in adjusting and regulating our color perception. There are many reasons for this. Beyond constancy, a second is coding efficiency. The dynamic range of any neuron is limited and must be adjusted to optimize the information it conveys. This includes matching the dynamic range of the neural response to the range of inputs, and also decorrelating the responses across neurons to remove redundancies in their responses. In fact this decorrelation has been a major theoretical argument for why the visual system recodes the cone responses – which are very highly correlated – into separate luminance and chromatic mechanisms (Buchsbaum & Gottschalk, 1983). Arguments based on coding efficiency successfully predict many of the characteristics of the early visual system, and of color coding in particular (Atick, 1990; Olshausen & Field, 1996).

The adaptation and response states in the visual system are in turn set by the characteristics of the visual environment, for they must efficiently represent the world at hand. A number of studies have examined the color statistics of natural images (Burton & Moorhead, 1987; Nascimento, Ferreira, & Foster, 2002; Olmos & Kingdom, 2004; Parraga, Troscianko, & Tolhurst, 2002; Ruderman et al., 1998; Tkacik et al., 2011; Wachtler, Lee, & Sejnowski, 2001; Webster & Mollon, 1997). Analyses of these statistics have shown that they can predict several properties of the visual responses to color. For example, in natural color gamuts most surfaces are desaturated or close to the mean luminance and chromaticity of the scene. To efficiently represent the contrast distribution, neural responses should be steepest around the mean level to allow fine discrimination among frequently occurring stimuli, while asymptoting at extreme levels where the chance of encountering a stimulus is low. This predicts the basic sigmoidal shape of neural responses and the fact that color discrimination is best for low contrasts, or changes around gray (Laughlin, 1981). Natural color gamuts and natural variations in daylight also tend to vary more along bluish-yellowish axes. Normalization to this property predicts that we should be less sensitive to blue-yellow contrasts, and there are several studies supporting this. Variability in achromatic settings within and between observers is greatest along the blue-yellow axis (Bosten, Beer, & MacLeod, 2015; Chauhan et al., 2014), and both threshold discrimination (Nagy, Eskew, & Boynton, 1987) and suprathreshold salience can also show weaker sensitivity for blue-yellow (Juricevic, Land, Wilkins, & Webster, 2010; McDermott, Malkoc, Mulligan, & Webster, 2010; Switkes, 2008). Neural responses in primary visual cortex as measured by fMRI are also weaker along blue-yellow than reddish-greenish axes equated for their component contrasts along the cardinal axes (Goddard, Mannion, McDonald, Solomon, &

Clifford, 2010). Finally, this blue-yellow insensitivity is evident in many uniform color spaces, in which the distances between stimuli are scaled to correspond to equal perceptual differences (McDermott & Webster, 2012b). In these spaces contrasts are elongated along the blue-yellow axis (Figure 11). Uniform color metrics – which are widely used in applications like color rendering - are usually developed empirically without regard to underlying theories or mechanisms of color coding (that is, they are designed to predict, but not to understand, color appearance). However, the foregoing suggests that such metrics could instead be constructed by starting with natural image statistics and then asking how these should be transformed into efficient representations, and this approach also leads to a perceptual scaling of color that corresponds closely to standard uniform metrics (Smets, Whitehead, & Webster, in review).

Figure 11. Uniform color distances plotted in the cone-opponent space. Large stimulus changes are required in bluish-yellowish directions, implying weaker sensitivity to the blue-yellow direction.

Adaptation also provides the critical link between the color statistics of the world and color experience of the observer. The stimulus that appears gray is presumably the average spectral stimulus we are exposed to. An observer with a higher lens pigment density will be exposed to a different spectrum on average, but because each individual is normalized for the prevailing mean the adaptation will again tend to compensate for their idiosyncratic sensitivity, so that both observers should tend to see the same distal stimulus as gray. That is, to the extent that two observers are exposed to the same environment, many aspects of their perception – and especially the norms in their percepts – should tend to agree (Webster, 2015). This implies that adaptation also supports a form of "inter-observer" constancy – imposing shared representations insofar as we are adapted to a shared environment.

However, the same processes predict that observers should experience color differently if the worlds they live in differ. Color statistics can vary widely across different environments. For example, in scenes dominated by lush vegetation the color distributions tend to be more aligned with the SvsLM chromatic axis, while in more arid and panoramic scenes the gamut is instead rotated toward the blue-yellow axis (Ruderman et al., 1998; Webster & Mollon, 1997). These produce different patterns of adaptation, each selective for the prevailing contrasts in the environment (Webster & Mollon, 1997) (Figure 12). Such effects could partly underlie supposed cross-linguistic differences in color naming, for the range of variation in focal color choices across languages is similar in magnitude to the theoretical range predicted simply by adapting the same speaker to different environments (Webster, 2014). The same environment can also vary over time. For example, color distributions change systematically with the seasons, predicting that color percepts might also show seasonal variations (Webster, Mizokami, & Webster, 2007). This has recently been demonstrated by showing that unique yellow settings reliably differ when tested in winter and summer (Welbourne, Morland, & Wade, 2015).

Figure 12. Simulations of how color appearance might be adapted to the colors specific to different environments (Webster, 2014).

Material perception

Color appearance is important because it informs us about the properties of a surface – e.g. whether a fruit is ripe or rotten or a complexion pallid or flush. This knowledge is critical for effectively interacting with our environment. Yet color is only one of many attributes that signal what we are seeing. A major recent trend in vision science has been the broader study of material perception (Fleming, 2014). This work is merging color and lighting with other cues such as texture, shape, and motion to understand how we identify and classify what objects are made of. It is not a coincidence that this field is also emerging at a time when computer graphics is allowing physics-based models to be used to create accurate visual simulations of objects defined by specific shapes and materials and illuminated in specific ways. As suggested by the adjectives we use to describe them, the attributes of materials vary widely and far beyond simple descriptions of their reflectance such as hue, saturation, and lightness. They can appear wet, dry or sticky; hard or soft; brittle or spongy; dull or lustrous; or rough or smooth. Individuals can rapidly and reliably judge these material properties (Fleming, Wiebel, & Gegenfurtner, 2013; Sharan, Rosenholtz, & Adelson, 2014), and thus an important issue is how color and other cues combine to support these percepts.

One aspect of material perception that has received extensive attention is the perception of gloss (Figure 13). Surface reflectance includes a mixture of diffuse and specular components that vary with the material. A matte surface is primarily diffuse while a glossy surface has pronounced specular highlights. Most of our understanding of color vision has been based on matte (Lambertian) surfaces. However highlights are common and have been emphasized previously as a cue to the spectrum of the illumination (D'Zmura & Lennie, 1986). They also provide powerful cues to the nature of the object that lead to perceptually salient differences and can be tied to different neural representations (Sun, Ban, Di Luca, & Welchman, 2015). Motoyoshi et al showed that in glossy surfaces the distribution of luminance levels is more skewed and that the degree of skewing biases whether an observer perceives a material as glossy or matte (Motoyoshi, Nishida, Sharan, & Adelson, 2007). Moreover, they found that skew is a feature that can be adapted. This work was influential in suggesting that material percepts could be based on simple statistical features of the images rather than an explicit model of the object's reflectance. However, this idea has been challenged by other work showing that such statistical descriptors fail to predict the percepts and that the judgments can be strongly affected by factors such as three-dimensional shape and where on the surface the specular highlights occur (Anderson & Kim, 2009; Ho, Landy, & Maloney, 2008; Marlow, Kim, & Anderson, 2011; Olkkonen & Brainard, 2010). Variations in specular information can also alter perceived shape (Mooney & Anderson, 2014) and pose a number of additional perceptual challenges. The binocular disparities of highlights need not correspond to the actual surface and thus must be discounted (Muryy, Welchman, Blake, & Fleming, 2013), while motion of the highlights changes in complex ways as the position of the object or lighting varies (Doerschner et al., 2011). Thus the perception of gloss appears to depend on a wide variety of perceptual processes that interact with percepts of shape and lighting.

Figure 13. Variations in the appearance of a surface from rough to smooth or matte to (Fleming, 2014).

Research is beginning to explore many other aspects of material perception, such as nonrigid materials like liquids and gels (Kawabe, Maruya, Fleming, & Nishida, 2015) or how we perceive changes as a material rots or decays (Zaidi, 2011). Specific exemplars of materials can vary widely, and the same material can appear very different under different viewing conditions. Thus how we are able to identify materials is challenging and may again involve multiple levels of analysis, from low-level summary statistics to high-level inferences about surfaces and viewing geometries. An important theoretical issue is whether and to what extent the perception of materials involves trying to model the causal physics of the world versus the more modest but tractable goal of representing how the visual properties of different materials vary under different viewing contexts (Anderson, 2015; Fleming, 2014).

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Color signals involved in other visual tasks

Thus far we have focused on studies examining the mechanisms of color appearance and the perception of surface properties. However as we noted above, the signals from the receptors must be used in service of all visual tasks, and similarly, color differences provide far more potential information than what something is, for they also carry critical cues to its shape and location. Many studies have explored the role of color in spatial and temporal vision (Shevell & Kingdom, 2008). Early work pointed to a strong modularity of visual processing, with chromatic signals largely segregated within different pathways from the visual areas encoding many aspects of form and motion. Supporting this, spatial and temporal acuity is substantially worse for pure color or equiluminant patterns (e.g. red and green stripes adjusted to have the same luminance) (Mullen, 1985), and the perception of motion in particular appears degraded under equiluminant conditions (Cropper & Wuerger, 2005). Moreover, these differences tended to mirror the properties of cells within different visual streams (Livingstone & Hubel, 1988). Nevertheless, color differences can support many perceptual judgments, including shape discriminations and movement (Shevell & Kingdom, 2008), and cortical neurons sensitive to color are also often selective for spatial frequency and orientation, thus carrying information about color and form. This spatial selectivity requires an important further transformation in the cortex to form double opponent receptive fields (i.e. cells that receive opposing inputs not only between the center and surround but also within each subregion) (Shapley & Hawken, 2011).

Color is also among the most salient cues in perceptual organization (Wolfe & Horowitz, 2004). This can be seen in standard plate tests for color deficiencies, which display numbers or shapes by using discrete dots that have the same chromaticity but vary in lightness. For a color-normal observer, it is easy to segregate the target from the background based on the color differences. And in the same way, it is much easier to spot a fruit among the dappled background of foliage when the target and leaves differ in color. In fact the salience of color may be especially important in natural contexts like this where there can be strong variations in light and shading (Mollon, 1989). Shadows tend to introduce large changes in luminance while much smaller changes in chromaticity. Consequently, an edge that varies in lightness but not chromaticity is more likely to correspond to a shadow, while a change in chromaticity is more likely to be seen as an object boundary (Kingdom, 2008). Such results suggest that one of the main functions of color vision is in fact to support spatial vision.

There remain however striking differences between vision with luminance and color-defined edges. For example, luminance edges often capture the spatial structure of scenes. The visual system is sensitive to spatial blur defined by luminance or chromatic contrast (Wuerger, Owens, & Westland, 2001). Yet in a full color image, blurring only the luminance contrast causes the image to appear blurred, while blurring only the chromatic components is almost imperceptible (Wandell, 1995). Color also tends to fill-in between luminance-defined edges. These effects form the basis of some dramatic visual illusions. In the watercolor effect (Figure 7b), colors added to luminance edges spread into the intervening uniform regions (Pinna et al., 2003). Similarly, the colors seen in afterimages are much more striking when they are contained by a luminance border. In fact, the same afterimage can appear a very different color when luminance borders delineate different regions that capture image locations that were adapted to different average colors (van Lier, Vergeer, & Anstis, 2009). Color cues are also poor at supporting several different higher-order percepts such as symmetry (Morales & Pashler, 1999) or shape from shading (Shevell & Kingdom, 2008).

Again the latter is not unexpected because color differences are more likely to be attributed to the object than the lighting.

In face perception, color provides reliable cues to emotional expressions and also to gender, and variations in color can impact attractiveness judgments (Changizi et al., 2006; Jones, Little, Burt, & Perrett, 2004; Nestor & Tarr, 2008). However these cues are generally weak compared to shape information. Face detection and identification is particularly sensitive to the luminance polarity cues around the eyes and brows – to dark pupils on light sclera. When this contrast is inverted, as in a photographic negative (Gilad, Meng, & Sinha, 2009), or shown as a chromatic rather than luminance difference (Paras & Webster, 2013), the appearance of the stimulus as a face is greatly diminished (Figure 14). This suggests that at least some processes underlying face perception are essentially color blind.

Figure 14. A noise image with symmetric luminance but random color appears symmetric and faces can be seen with dark spots for eyes. These percepts are lost when the image is instead symmetric in color but random in luminance (Paras & Webster, 2013).

However, color may be highly relevant in other ways. Face perception is often considered a very high-level perceptual capacity, but one which may share striking similarities with color in terms of the underlying coding scheme (Webster & MacLeod, 2011). Many current models postulate a "face space" analogous to color space, where an individual face is represented by a vector or identity trajectory specifying the direction (~hue) and distance (~saturation) relative to the prototypical face or norm (~gray) (Valentine, Lewis, & Hills, 2015). Consistent with this, caricatures amplify the distance from the norm along the same direction in the space, equivalent to turning up the saturation of a given hue. Moreover, adaptation to an individual face alters the appearance of subsequent faces in ways that are also very similar to chromatic adaptation, potentially resetting the norm according to the faces were are currently exposed to (Webster & MacLeod, 2011). Finally, color and face processing may involve similar parallel architectures along the ventral stream (Lafer-Sousa & Conway, 2013). These correspondences are important because they suggest that the visual system may often uses the same strategies to represent very different stimulus attributes. In this regard, our evolving understanding of color – a system which is highly complex yet in some ways much more tractable because the number of underlying dimensions is at least small and known with great accuracy – has the potential for broad impact, for the principles we discover are likely to be relevant to a wide range of sensory processes.

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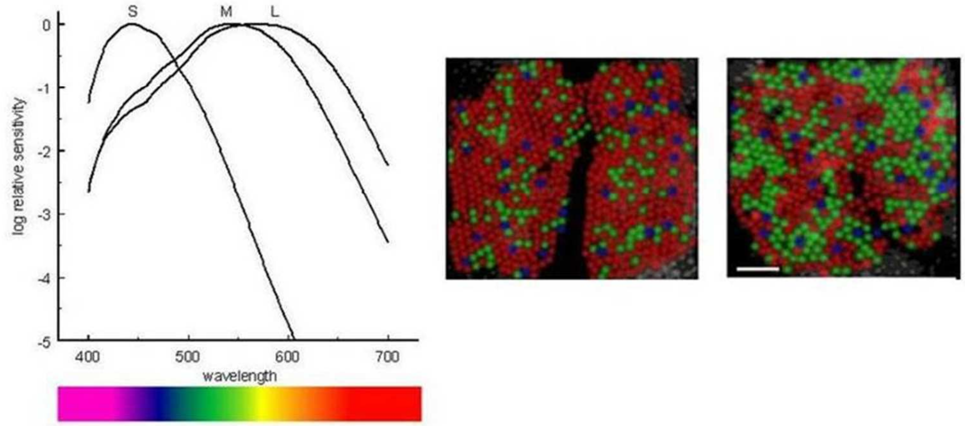

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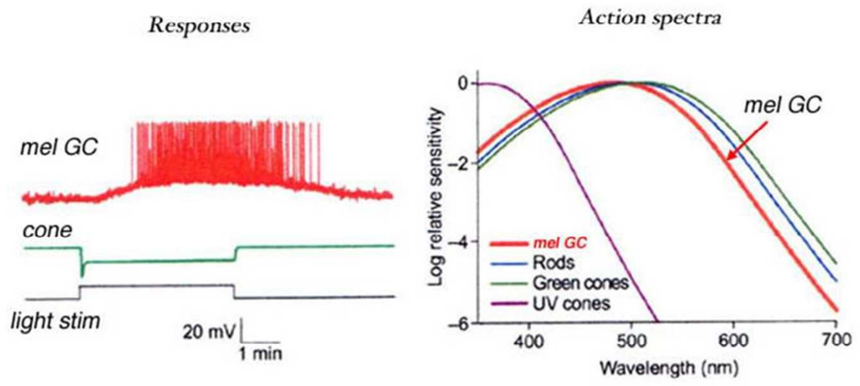

Fig. 50. The physiological responses of melanopsin ganglion cells to light. The response on the left shows the melanopsin cells slow onset steady state depolarizing spiking that occurs to a light flash as compared the slow but faster onset hyperpolarization of the green cones in the mouse retina. The action spectra to the right show the melanopsin ganglion cell to have a peak sensitivity to light of 484 nm compared with the rods and other cone types in the mouse. After Berson, 2003.

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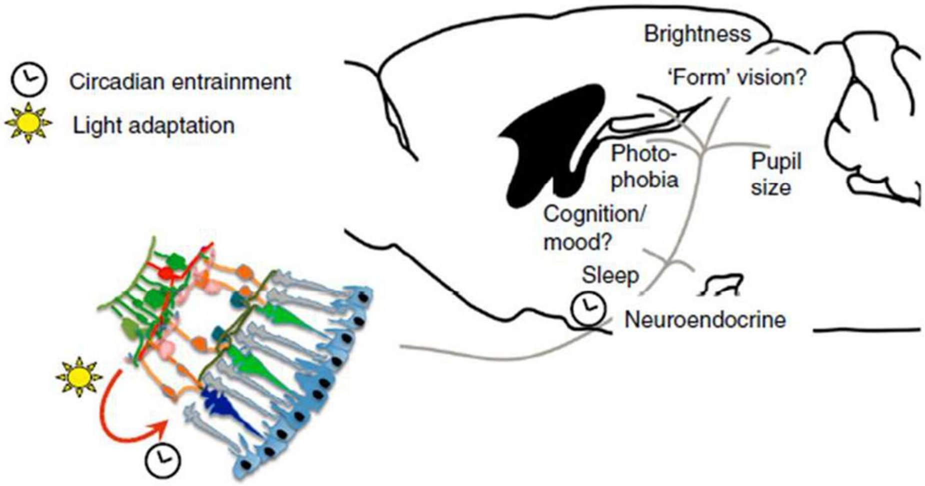

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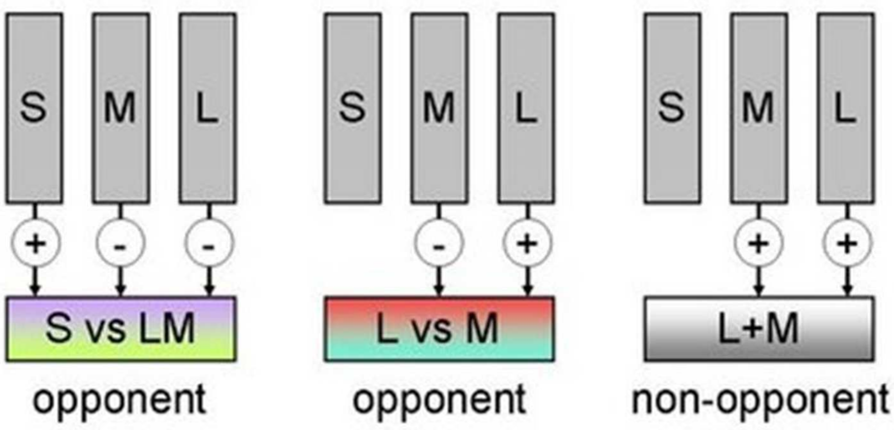

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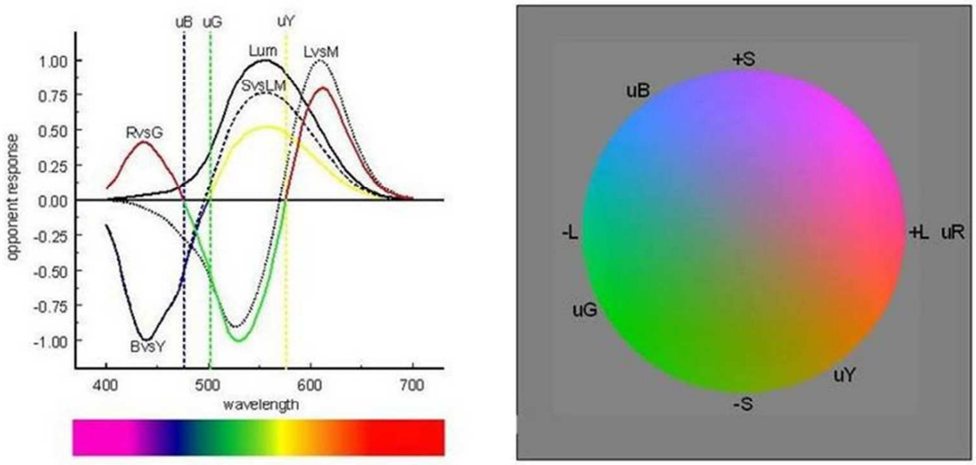

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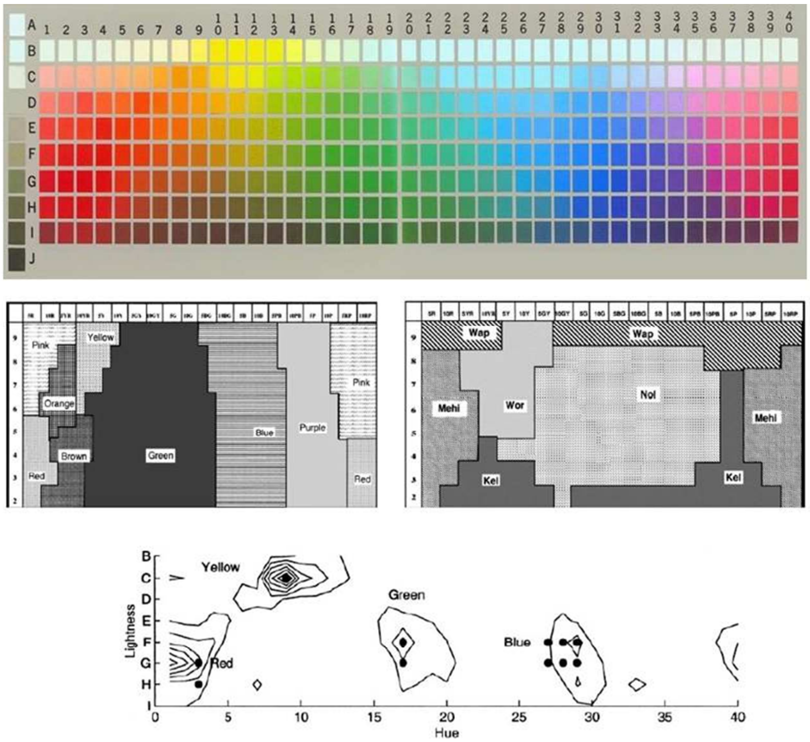

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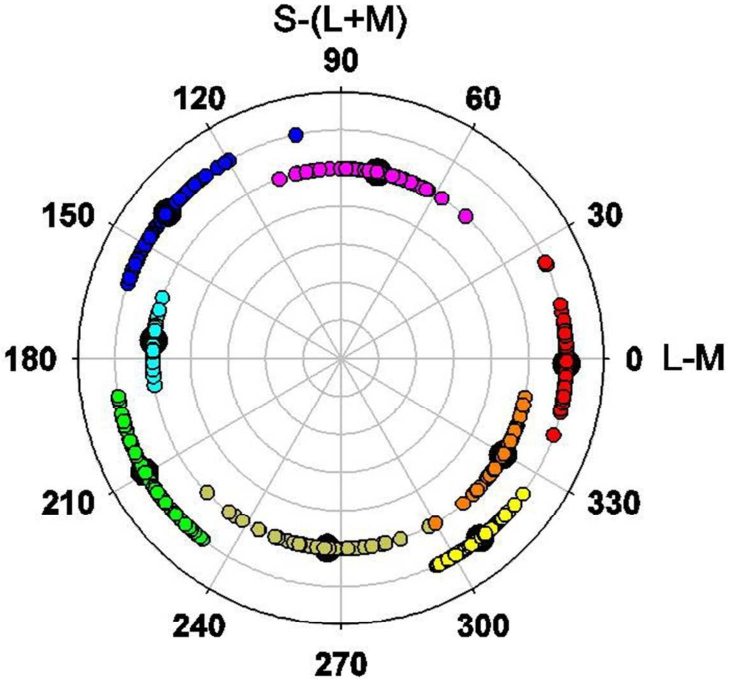

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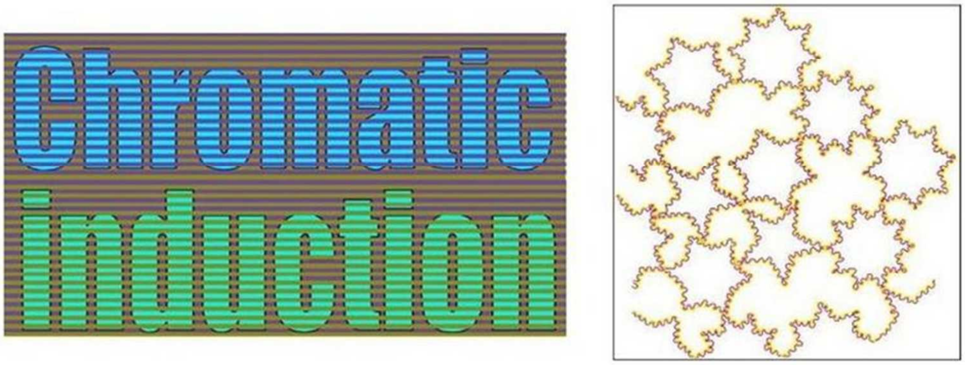
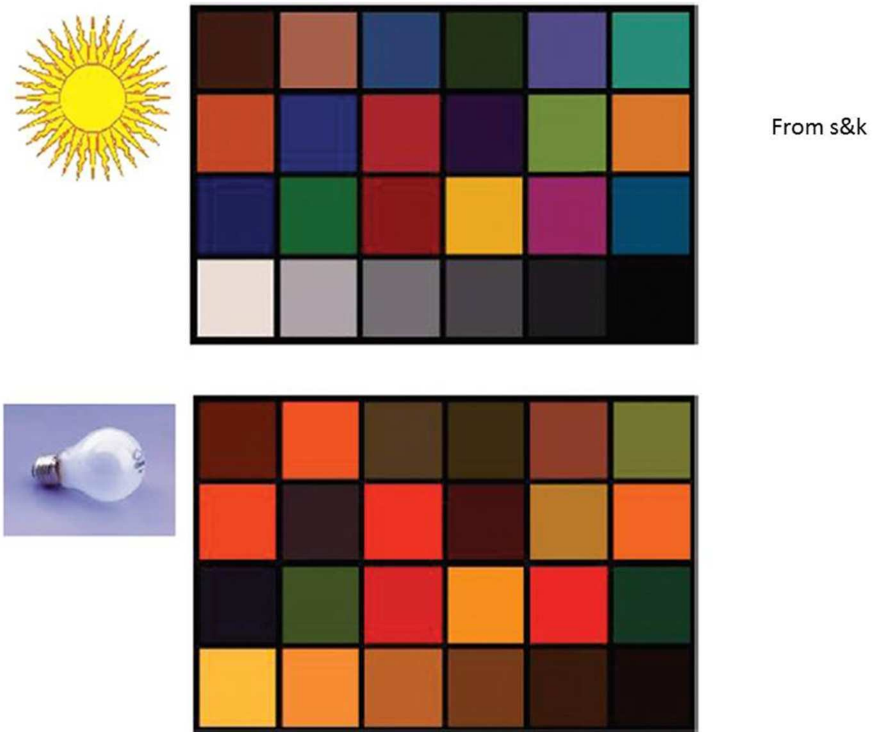


254x190mm (96 x 96 DPI)



254x190mm (96 x 96 DPI)

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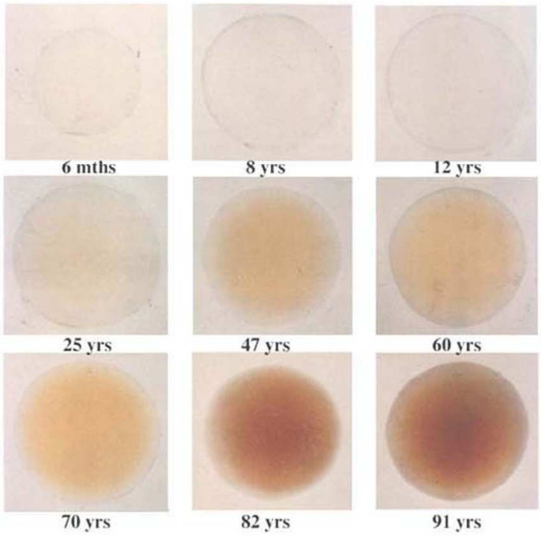
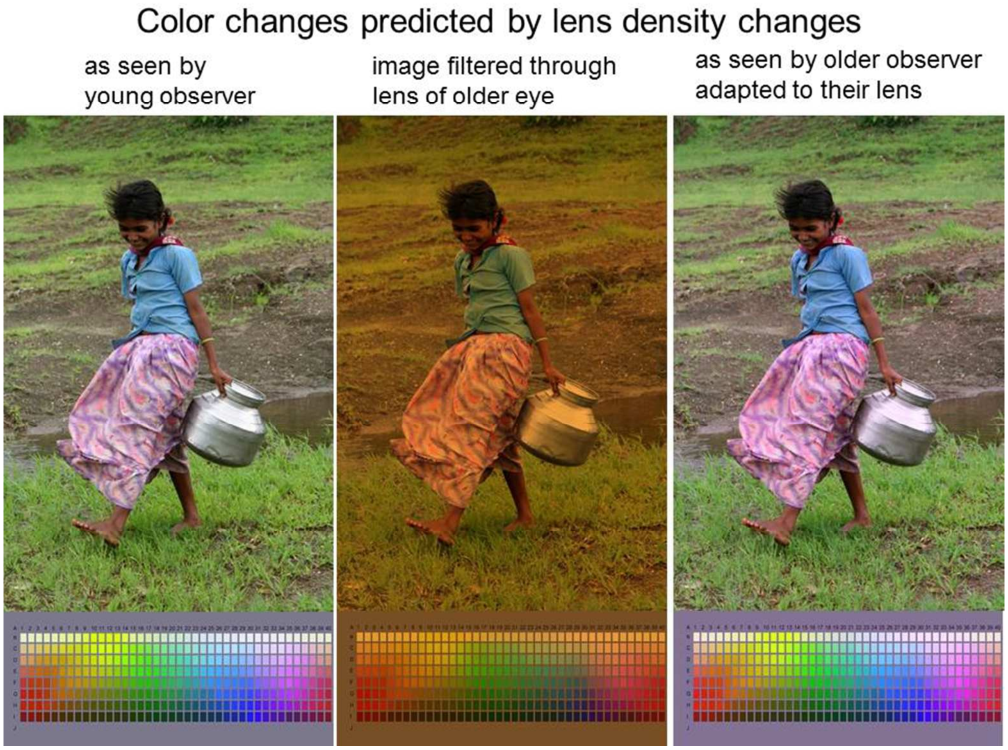
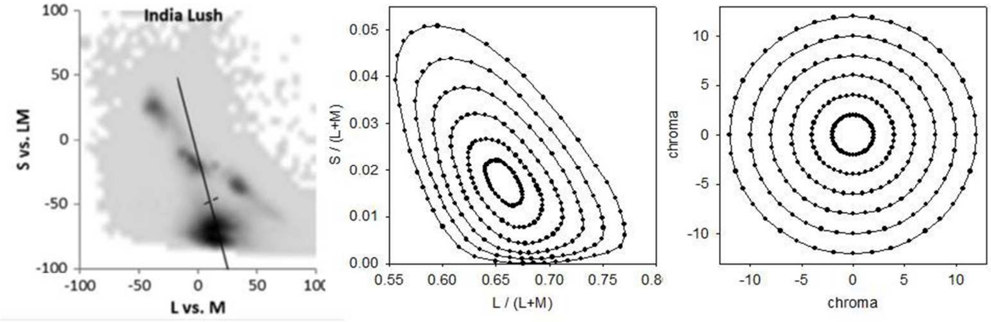

Changes in lens pigmentation with aging

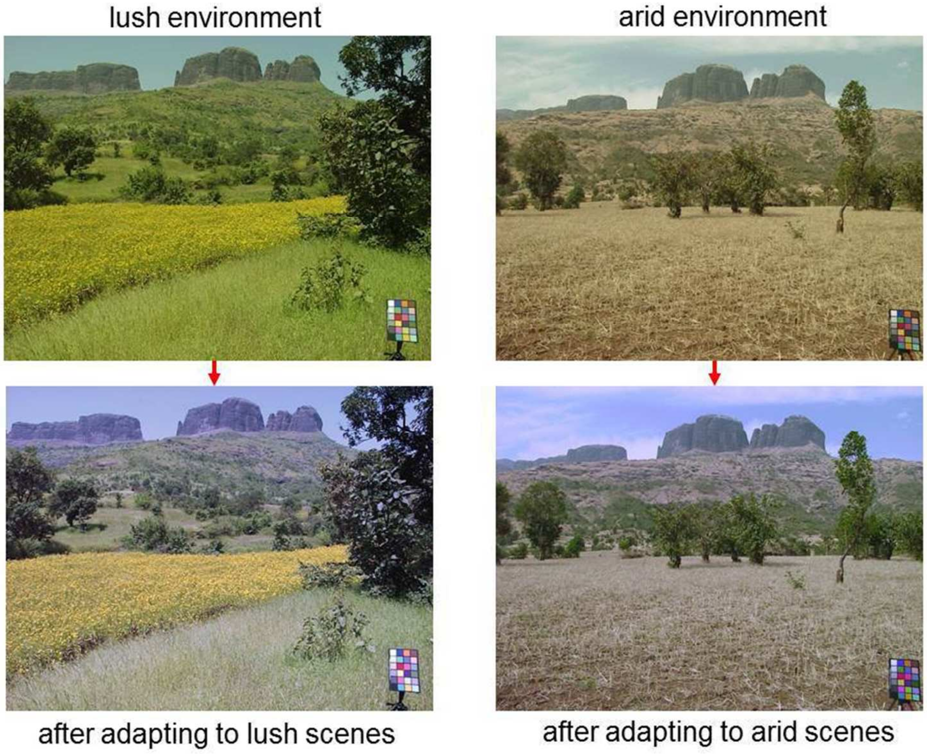
254x190mm (96 x 96 DPI)



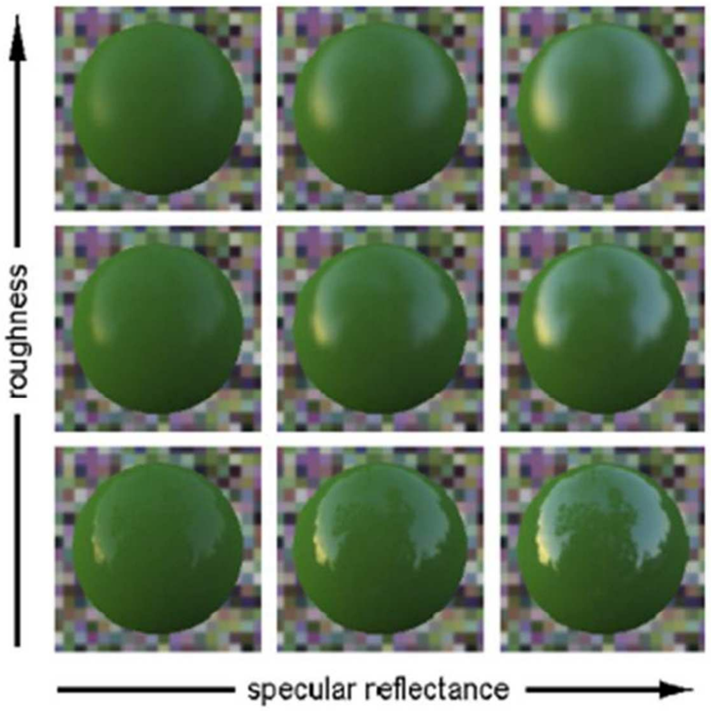
254x190mm (96 x 96 DPI)



254x190mm (96 x 96 DPI)



254x190mm (96 x 96 DPI)



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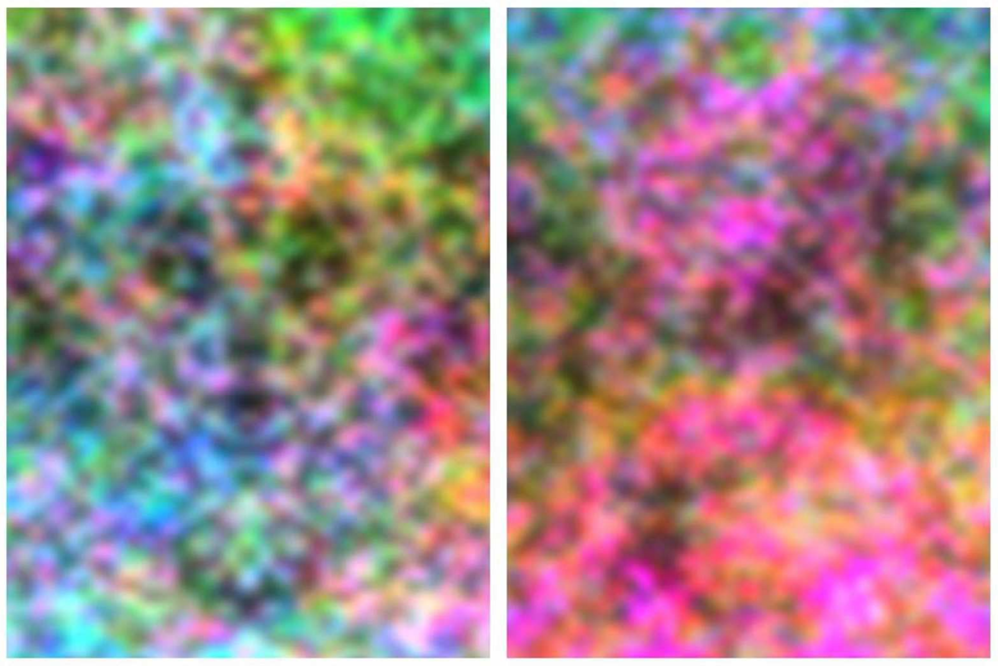

254x190mm (96 x 96 DPI)