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Do You See What I See? Diversity in Human Color Perception

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Abstract

In our tendency to discuss the objective properties of the external world, we may fail to notice that our subjective perceptions of those properties differ between individuals. Variability at all levels of the color vision system creates diversity in color perception, from discrimination to color matching, appearance, and subjective experience, such that each of us lives in a unique perceptual world. In this review, I discuss what is known about individual differences in color perception and its determinants, particularly considering genetically mediated variability in cone photopigments and the paradoxical effects of visual environments in both contributing to and counteracting individual differences. I make the case that, as well as being of interest in their own right and crucial for a complete account of color vision, individual differences can be used as a methodological tool in color science for the insights that they offer about the underlying mechanisms of perception.

> . . .our ideas of colors. . .excited by the same object may be very different in themselves, without our being aware of it; and that we may nevertheless converse intelligibly concerning such objects, as if we were certain the impressions made by them on our minds were exactly similar.
>
> —John Dalton (1798, p. 28)

1. INTRODUCTION

Individual differences in color vision first entered the academic literature in 1798, when John Dalton proposed that the underlying cause of the abnormal color vision that he and his brother experienced was a blue tint of the vitreous humor, causing it to absorb light of medium and long wavelengths. In the written account of a talk given to the Manchester Literary and Philosophical Society in 1794, Dalton (1798, p. 28) described his realization of the "peculiarity" of his color vision. Having studied botany, he had noticed that he had difficulties identifying flowers by their colors, but he had already studied the physics and optics of light before he realized by chance that his perception of a large color change in a flower under a change in illumination was shared with his brother but not with the majority of people. Dalton donated his eyes to medical science, and his theory concerning the vitreous humor was quickly disproved at autopsy. Some 150 years later, DNA was extracted from his eyes and sequenced, and Dalton was found to have been a dichromat, lacking one of the three normal cone types (Hunt et al. 1995).

Dalton's observation that we assume that our perceptions are consistent with those of others around us is as true today as it was then. Numerous sources of variation in the human apparatus for color vision put each of us in distinct perceptual worlds, yet even differences that have a substantial impact on perception can remain undetected. As Dalton says, we converse about our surroundings in language that implies that they have objective, fixed properties, ignoring the fact that our perceptions, which may vary between individuals, are what confers our sense of those supposedly fixed properties. The label "blue" might well describe a short-wavelength-biased object reflectance spectrum but may conceal a variety of underlying percepts among different observers. The assumption that our perceptions correspond to an objective reality hardly gives us motivation to discuss them, and lack of discussion hides individual differences in perception from view as a phenomenon for investigation. When a stimulus such as #theDress (see Section 7) comes along that serendipitously reveals a huge difference in color perception across individuals, it is nearly as surprising to color scientists as it is to the general public. Individual differences are often suggested in psychophysical data and may be noted by researchers but are less often the target of research themselves. Compounding the problem, as argued by Olkkonen & Ekroll (2016), is publication bias: The presence of large individual differences in data sets may be viewed as an indication that something is wrong with the study, giving researchers cause to distrust the study's presentation of the averages that they generally care about.

Although I argue in this review that individual differences are underappreciated and not fully explored or exploited for the insights that they can offer about the mechanisms of color perception, it is also fair to say that diversity in color perception is better understood and appreciated than diversity in other perceptual domains. Congenital X-linked red–green color vision deficiency (CVD), to which Dalton now lends his name, is caused by variations in an array of genes responsible for encoding the medium (M)- and long (L)-wavelength-sensitive opsins. Investigations into genetic variation at this locus and its perceptual consequences have provided a rich understanding of how, in addition to the loss of entire genes, single nucleotide substitutions can impact color vision (see Section 2). Also well characterized is variation in prereceptoral filtering by the lens and macular pigment (see Section 2.9), which, together with characterized

variation in receptor sensitivities, allows the development of models of receptor responses to colored stimuli for individual observers.

Despite this well-described diversity in predicted receptor responses to colored stimuli, the concept of a standard observer in color science persists. Color spaces built on standard observer color matching functions or photopigment spectral sensitivity functions are typically constructed from data averaged over many individuals, but they may not provide an accurate model of the color vision of a particular individual, even if they are a normal trichromat possessing the three normal cone types. Standard observer color spaces are used to calculate colors for display in print or via screens or projectors that match the spectra reflected by objects in the external world. Such metameric matches for a standard observer will be mismatched for another with different visual apparatus, a problem that is becoming more prominent as display primaries become spectrally more narrowband to enlarge color gamuts (see Section 5).

Beyond differences at the input stage of color vision (receptor activities), there are individual differences in the representations of color at all levels of the visual system, affecting every aspect of color perception, from discrimination to constancy, appearance, naming, and presumably subjective color experience (see Sections 6–8). To what extent individual differences in tasks thought to draw on higher-level color representations are directly inherited from downstream differences in the peripheral color vision system, and to what extent they arise from differences in retinogeniculate or cortical mechanisms of color perception (see Section 3), are questions of active research.

As well as being genetically influenced, it is thought that color vision can be impacted by long-term adaptation or calibration to sensory environments (see Section 4). The consequences of this for individual differences are complex. On the one hand, calibration to different sensory environments may induce differences in color perception in long-term inhabitants of those different environments, but on the other hand, calibration to a common sensory environment may reduce the impact on perception of individual differences in the low-level mechanisms of color vision. Such adaptation or calibration may help to explain why seemingly large differences in color matches (observer metamerism) may not translate to equally tangible differences in the ways in which different individuals describe color appearance.

Individual differences are a subject of interest in their own right, but they can also be exploited by the researcher as a tool for understanding the neuroscience of color perception (Mollon et al. 2017, Wilmer 2008; see Section 9). For example, correlational studies across individuals have the potential to uncover and unify explanations of visual traits at different levels, e.g., genetic and behavioral. Data dimension reduction techniques can identify factors underlying individual differences in a set of visual traits, providing insights into the traits' underlying mechanisms. Although there is growing interest in using individual differences as a tool for sensory and cognitive neuroscience in this way, for the most part, variability is still discarded from analysis as noise. In addition to adding analyses of individual differences into future research plans, researchers could mine the trove of existing data sets for the insights offered by unanalyzed individual variability.

In this review, I aim to summarize what we know about individual differences in color vision, focusing on variations among normal trichromats and those caused by congenital CVDs (for a review of acquired CVDs, see Simunovic 2016). I first consider individual differences in the neural mechanisms at different levels of the color vision system and their determinants (Sections 2–4), and then discuss functional variation in color matching, discrimination, and appearance (Sections 5–8) but not color preference (see Hurlbert & Ling 2007, Schloss & Palmer 2017, Taylor et al. 2013). I try to explain the relevance of individual differences in color perception for a broad audience and make the case that greater attention to individual variation could speed and enhance progress in color science.

2. INDIVIDUAL DIFFERENCES IN PHOTORECEPTORS AND OCULAR FILTERING

Normal trichromatic color vision depends on three classes of cone. S cones are maximally sensitive in the short-wavelength part of the spectrum, M cones at medium wavelengths, and L cones at long wavelengths. However, receptor activities in response to colored light are highly polymorphic among individuals owing both to variations in cone photopigment sensitivities, especially for the M and L photopigments, and to variations in ocular filtering in the optical densities of the lens, of macular pigment, and of photopigment molecules in cone outer segments.

2.1. Diversity in the M and L Opsin Gene Array

Duplications of an ancestral gene for a long-wavelength-sensitive opsin and divergence in spectral sensitivity of duplicate genes from the original have relatively recently (fewer than 40 million years ago) provided Old World primates and some species of New World primates with trichromatic color vision. Normal human trichromats possess one copy of an L opsin gene followed by one or more copies of an M opsin gene in an array at Xq28. Upstream of the first gene in the array is a locus control region (LCR). It is thought that only the first two opsin genes in the array are close enough to the LCR to be expressed. *OPN1LW* and *OPN1MW*, the genes for the L and M opsins, respectively, are 98% homologous, meaning that there are frequent misalignments during recombination and therefore a relatively high number of mutations (Hunt & Carvalho 2016, Neitz et al. 2019).

2.2. Deuteranopia and Protanopia

Unequal crossing-over events have led to deletions of M or L opsin genes such that, for approximately 2% of X chromosomes, there is a single functional opsin gene in the array, rather than the usual two or more. Males with these genotypes are protanopic (if an M opsin gene is present) or deuteranopic (if an L opsin gene is present). Because they have only one photoreceptor class sensitive in the medium- and long-wavelength parts of the spectrum, dichromats accept any ratio of red and green light in making a Rayleigh match to a narrowband yellow light. They confuse colors along characteristic protan or deutan confusion lines in color space and are assumed to have one-dimensional color vision (i.e., relying on S versus L or S versus M signals).

2.3. Monochromacy

If the genes for both the L and the M opsins are missing or nonfunctional, then the result is X-linked S-cone monochromacy, affecting approximately 1 in 100,000 males (Gardner et al. 2009, Pokorny et al. 1979). Other forms of monochromacy result from the presence of rods only (Pokorny et al. 1979) or (very rarely) L or M cones only (Sharpe et al. 1999, Weale 1953). In monochromacy, the single receptor type cannot distinguish a change in wavelength from a change in intensity (the principal of univariance; Rushton 1972), so there are no signals with which to reliably discriminate color. Unlike dichromats, monochromats have achromatic vision and can have further visual difficulties at high light levels and/or with spatial acuity, depending on the missing cone classes.

2.4. Deuteranomaly and Protanomaly

If an individual expresses two opsin genes from the same class instead of the usual M and L opsin genes, or if they express one normal L or M opsin gene and one hybrid gene containing genetic elements of both (for discussions, see Bosten 2019, Neitz & Neitz 2011), then they have anomalous

trichromatic color vision. Deuteranomals (approximately 5% of males and <0.5% of females; Birch 2012) possess two cone types similar in sensitivity to the normal L cone (L and L′), while protanomals (approximately 1% of males and 0.01% of females; Birch 2012) possess two cone types similar in spectral sensitivity to the normal M cone (M and M′). Color vision is trichromatic, but color perception is different than that of normal trichromacy.

2.5. Other Polymorphisms of the L and M Opsin Gene Array

The L and M opsin gene array contains a large number of single nucleotide polymorphisms (SNPs), but only six or seven are known to influence the spectral sensitivity of the opsins (Neitz & Neitz 2011). Of these, two SNPs create 20 nm of the difference in spectral sensitivity between the L and M cones, and the allele present at these locations determines the cone class (Neitz & Neitz 2011). Variation at the other locations leads to individual differences in cone spectral sensitivities. The most well-studied genetic polymorphism of color vision within normal trichromats occurs at site 180 of the opsin: If the more common (56%) serine is present, then the photopigment's peak spectral sensitivity is shifted 3 nm to longer wavelengths than if alanine is present (Sharpe et al. 1999). The few studies that have tackled the question of the functional consequences of polymorphisms of the L and M opsins among normal trichromats show that these polymorphisms can have measurable effects on perception. Winderickx et al. (1992) showed that normal trichromats' Rayleigh matches are influenced by the site 180 polymorphism, and Dees et al. (2015) found that the same polymorphism influences spatiochromatic contrast sensitivity for deutan and protan stimuli.

2.6. Heterozygotes for Polymorphisms of the L and M Opsin Gene Array

Female heterozygotes with polymorphic versions of the L and M opsin gene array are a diverse group. Carriers of dichromacy or anomalous trichromacy (approximately 16% of women) possess genes for two normal opsins on one X chromosome; however, on the other X chromosome, they possess a gene for only one opsin (for carriers of dichromacy) or genes for two opsins of the same class (for carriers of anomalous trichromacy). X-chromosome inactivation means that the retina expresses a patchwork of the genotypes of the two X chromosomes separately (Jordan & Mollon 1993, Sharpe et al. 1999), so one normal opsin gene is missing in (on average) half of receptors. Consequently, carriers tend to have L:M cone ratios that are more extreme than those of normal trichromats (see Section 2.8), affecting wavelength-specific luminance perception (Schmidt's sign). Since carriers of red–green CVD express three normal cone types (albeit with one missing from approximately half of the retina), their color vision is usually normal trichromatic. However, in addition to altered luminance perception, carriers can show subtle differences in color perception compared to homozygotes for normal trichromacy. At very short stimulus presentation times (which presumably preclude sampling by multiple patches of retina, including some that have normal cone types), they may misname colors and have difficulty resolving pseudoisochromatic plates (Cohn et al. 1989). Even at standard presentation times, carriers may show significantly more errors on diagnostic tests for CVD than do noncarriers (Dees & Baraas 2014). Rarely, carriers may express full CVD themselves (Feig & Ropers 1978, François & Verriest 1961). This manifesting heterozygote phenotype has been proposed to occur when the X chromosome carrying both L and M opsin genes is inactivated over the whole retina (Jordan & Mollon 1993, Sharpe et al. 1999). Consistent with this, extremely rare heterozygotes have been found to show CVD in one eye only (for a review, see Feig & Ropers 1978), and there are rare cases of monozygotic (MZ) twins or triplets where one sister has CVD and the other(s) show normal trichromacy (François & Verriest 1961, Jørgensen et al. 1992, Yokota et al. 1990). However, a recent genetic analysis of

a carrier of protan CVD with unilateral protanopia revealed an additional genetic defect in the M opsin promoter (Neitz & Neitz 2017), implying that additional genetic abnormalities may be required to account for the manifesting heterozygote phenotype.

Carriers of anomalous trichromacy or females heterozygous for different polymorphisms of the L and/or M opsin genes can express genes for up to two different versions of the L opsin and two different versions of the M opsin and therefore can have up to five distinct cone types, although the case of four cone types is more commonly discussed and has been recently reviewed (Jordan & Mollon 2019). If the additional cone types are functional, and if the brain has sufficient plasticity to segregate their signals independently without the need to evolve additional postreceptoral hardware, then color vision would be tetrachromatic (with four distinct cone types) or pentachromatic (with five). Although the majority of females possess at least four distinct opsin genes (Davidoff 2015, Jordan & Mollon 2019), the prevalence of strong tetrachromacy or pentachromacy [the ability to use the additional cone type(s) for extra dimensions of color vision] is unknown. The most common polymorphisms that confer additional cone types are subtle variations within cone classes, like the polymorphism at site 180. The presence of an additional cone class only approximately 3 nm spectrally distinct from its neighbor may not be sufficient to confer a functional dimension of color vision. Instead, the presence of a more spectrally distinct additional photopigment of the type that underlies mild anomalous trichromacy has been suggested to provide more plausible conditions for strong tetrachromacy (Jordan & Mollon 2019, Jordan et al. 2010); this photopigment phenotype is possessed by only a few percent of females. Another class of observer who may be well placed to make use of an extra M, L, or hybrid cone class is the polymorphic female anomalous trichromat. These women may possess two roughly equally salient color dimensions based on comparisons of the activities of three variants of a single cone class.

Despite secure expectations from genotyping for the large numbers of heterozygotes expected to possess four or more cone types, only a few studies have attempted to find evidence for strong tetrachromacy. Jameson et al. (2001) found that participants heterozygous for the site 180 polymorphism delineate the spectrum into more color bands than do homozygotes, although this difference in perception is not definitively attributable to strong tetrachromacy (Jordan & Mollon 2019). Jordan et al. (2010) identified one candidate for strong tetrachromacy who passed their two tests of color discrimination, and four out of nine carriers of anomalous trichromacy showed some evidence of tetrachromacy on one test. Considerable care must be taken in future studies to rule out alternative explanations for passing tests of tetrachromatic color discrimination, such as illusory texture perception conferred by patches of distinct gene expression on the retina (Makous 2007).

2.7. Variations of the S-Cone Subsystem

Compared to variations in the L and M opsin gene array, much less is known about variations in the S-cone subsystem and their consequences for perception. There are several reasons why this subsystem has been relatively neglected as a topic of research. First, as the ancestral color subsystem, it is more stable and less variable, being less prone to mutation than the subsystem relying on the L- and M-cones (Sharpe et al. 1999). Second, sex-linked genetically determined differences in color vision caused by variation in the X-chromosomal L and M opsin genes are more salient than differences that may be caused by variation in the autosomal S opsin gene. Third, the Rayleigh match, which has been useful in revealing the effects of polymorphisms of the L versus M subsystems, operates at long wavelengths and is designed to ignore the contribution of S cones. Last, differences in spectral sensitivity caused by the lens and macular pigment are in the same spectral region as differences that would result from variation in the S cones, and it is challenging to isolate these sources of variation.

Nonetheless, there are seven known mutations of the S-opsin gene that result in tritan (S-cone) CVD (Baraas et al. 2012, Gunther et al. 2006, Neitz et al. 2020). The phenotypes conferred are various, ranging from tritanopia to mild tritan defects (Neitz et al. 2020), with some defects progressing with age. In the case of heterozygotes for a mutation affecting site 190 of *OPN1SW*, there are mild tritan deficits at high luminance levels but tritanopia under relative dark adaptation (Baraas et al. 2012). Estimates of the prevalence of congenital tritanopia vary widely, from 1/65,000 (Wright 1952) to 1/500 (in some populations) (Went & Pronk 1985). Tritanomaly, defined as an alteration in the S-cone sensitivity function, seems to be even rarer (although note the possible reasons for underdiagnosis identified above). Some argue that its existence has not been satisfactorily demonstrated at all (Sharpe et al. 1999), and that people with tritan deficits who are not tritanopic are better considered to have incomplete tritanopia resulting from S cones with impaired function but normal spectral sensitivities (Smith 1973, Smith et al. 1973). However, Pokorny et al. (1981) tested 39 individuals with tritan deficits using a Moreland anomaloscope, an instrument designed to measure individual differences in blue–green matches, and found that at least 7 individuals had shifted but narrow Moreland matches; these results provided new candidate tritanomals in addition to one identified by Schmidt (1970).

2.8. Individual Differences in L:M Cone Ratio

In addition to individual differences in the spectral sensitivities of photoreceptor classes, there are huge individual differences in the relative numbers of L- and M-cones (much less is known about individual differences in the density of S cones, although variation does exist, for example, in enhanced S-cone syndrome; see de Carvalho et al. 2021). In different individuals, the ratio of L to M cones is approximately normally distributed (Carroll et al. 2002) and can vary from as little as 0.3 to as much as 16, as estimated using psychophysical or electroretinographic responses to chromatic flickering light (Kremers et al. 2000), retinal densitometry (Kremers et al. 2000), retinal imaging at the single-cone level (Hofer et al. 2005), or postmortem ratios of photopigment messenger RNA (Carroll et al. 2002). The underlying causes of individual differences in L:M cone ratio are not fully understood, but it is a heritable trait (Lutze et al. 1990), and genetic associates have been found (Gunther et al. 2008, Lawrance-Owen et al. 2014).

Perceptually, cone ratios affect the luminosity function and luminance perception (Miyahara et al. 1998, Rushton & Baker 1964); e.g., the relative perceived luminance of long-wavelength light increases with the proportion of L-cones. There is also a reduction in spatial acuity for cone-isolating stimuli if one cone type is much rarer than normal (Danilova et al. 2013, Miyahara et al. 1998). Beyond this, surprisingly little impact of the L:M cone ratio on color perception has been found (Neitz et al. 2002). Illustrative cases have been presented by Miyahara et al. (1998), who found that their carriers of protanopia, with extreme L:M ratios of $<0.1:1$, had normal color increment thresholds, had normal settings of unique (pure) yellow, and performed normally on a hue-scaling task that probes color appearance. Why do huge individual differences in the ratio of L- to M-cones have so little impact on color vision? One possibility is the presence of a calibration process of the type discussed in Section 4 that normalizes color perception (Neitz et al. 2002), perhaps via calibration to the color distributions of relevant stimuli in the external environment.

2.9. Variations in Lens, Macular Pigment, and Optical Density

There are individual differences in all of the main sources of prereceptoral filtering: macular pigment, lens, and the optical density of photopigment molecules in cone outer segments. Lens and macular pigment absorb light mainly at short wavelengths but vary widely in their densities, by approximately 0.6 log units for the lens (e.g., Coren & Girgus 1972, Pokorny et al. 1987) and 1 log

unit for macular pigment (e.g., Hammond & Caruso-Avery 2000, Yu et al. 2012). Individual differences in lens density are accounted for mainly by age: Lens density increases by approximately 0.1 log units with each decade of life (Pokorny et al. 1987, van de Kraats & van Norren 2007). Cumulative exposure to ultraviolet (UV) light (affected by latitude, altitude, cloud cover, and local ozone density, as well as by time spent outdoors) is highly correlated with age but independently influences lens density (Tomoda et al. 1990, Werner et al. 1990). Variance in macular pigment density is influenced by diet, specifically by intake of the carotenoids lutein and zeaxanthin (Hammond et al. 1996a, Nolan et al. 2007). Interestingly, it has been suggested that males have higher macular pigment density on average than females, secondary to physiological differences in the way in which carotenoids are processed (Hammond et al. 1996a), although this has not always been supported by evidence (Iannaccone et al. 2007). Individual differences in lens and macular pigment density are not independent, but instead are inversely correlated, with a shared variance of approximately 22% (Hammond et al. 1997). The correlation is influenced by age (Werner et al. 2000) but may also be affected by iris color (Hammond et al. 1996b, 2000) and dietary intake of carotenoids (Berendschot et al. 2002, Hammond et al. 1997). There are also genetic influences on prereceptoral filters: SNPs in four candidate genes involved in lutein absorption explain over 25% of the variance in both plasma lutein and macular pigment density (Borel et al. 2011). Genetic influences on age-related cataract may also influence nonpathological lens brunescence (Shiels & Hejtmancik 2015).

There are substantial individual differences in the optical density of photopigment within the outer segments of L- and M-cones, ranging between approximately 0.3 and 1 for the fovea (Renner et al. 2004), which are at least partly determined by genetic diversity within the opsin genes (Neitz et al. 1999, Renner et al. 2004). Photopigment spectral absorptance functions broaden as optical density increases because light near the preferred wavelength is selectively filtered as it travels through the cone outer segments. Individual differences in optical density therefore influence in vivo cone spectral sensitivity functions and, consequently, color matches and other aspects of color perception. There is so far only limited evidence that optical density can differ between the M- and L-cones (e.g., Burns & Elsner 1993; for a table, see **http://www.cvrl.org/database/text/optdens/optdens.htm**), but it has been proposed that this potential difference could help to account for the poor relationship between photopigment peak spectral sensitivities and color discrimination in anomalous trichromacy (Thomas et al. 2011). In addition, rare cases have been identified of dichromats who show trichromacy that is thought to rely on within-observer variation in optical density within a single cone class (Neitz et al. 1999). Published estimates of S-cone optical density range from 0.1 to 0.38 (Bowmaker & Dartnall 1980, Wyszecki & Stiles 1980), but data on individual differences are not available.

3. VARIATIONS IN POSTRECEPTORAL COLOR MECHANISMS

3.1. Retinogeniculate Color Pathways

Postreceptoral color signals have been thought to be carried by two dominant retinogeniculate pathways. The parvocellular pathway, originating in the midget retinal ganglion cells, carries information about medium- to long-wavelength (teal to red) chromatic contrasts by receiving opposing inputs from the M and L cones (Crook et al. 2011). The koniocellular pathway, originating in the small bistratified ganglion cells, carries information about short- to medium- and long-wavelength (violet to chartreuse) chromatic contrasts by opposing ON inputs from the S cones to OFF inputs from the other two cone types (Dacey & Lee 1994). More recently, an S-OFF pathway carried by the midget ganglion cells has been identified that shows variable chromatic tuning depending on the weightings of cone inputs to individual cells (Wool et al. 2019).

In contrast to individual differences in color perception caused by differences in receptor sensitivities and prereceptoral filtering, relatively little is known about individual differences in retinogeniculate color mechanisms and how they might influence perception. There is psychophysical evidence for individual differences in the orientations in color space of the cardinal retinogeniculate chromatic mechanisms S/(L + M) and L/(L + M) (Krauskopf et al. 1996, Webster et al. 2000a), although it is not clear to what extent the observed variation is inherited from differences in cones and prereceptoral filters (Smith & Pokorny 1995), or to what extent it is due to differences in the postreceptoral mechanisms themselves. Individual differences in discrimination thresholds for increments and decrements of S-cone contrast have been found to be reliably different (Bosten et al. 2014), implying that there are separate individual differences in the underlying S-ON and S-OFF mechanisms. Individuals with a genetic mutation to receptors specific to ON bipolar cells lack S-cone input to small bistratified ganglion cells yet have normal color perception (Dryja et al. 2005), challenging the standard model of retinogeniculate processing of S-cone signals (Neitz & Neitz 2014). The determinants of individual variation in postreceptoral retinogeniculate color mechanisms more broadly likely include a range of genetic factors. Recent evidence has revealed that mammalian retinal ganglion cells are clustered into subtypes by gene expression profile (Rheaume et al. 2018); these subtypes presumably correspond to known morphologically and functionally distinct classes (Peng et al. 2019). It seems likely that the same genetic differences that have driven diversity in retinal cell types across species (Baden et al. 2020) also influence within-species individual differences.

3.2. Cortical Color Mechanisms

In the cortex, color information is processed through early visual areas V1–V3. Downstream, there are thought to be areas that are specialized for color, or that are at least color biased, including V4 and V8 (and/or VO1 and VO2; Johnson & Mullen 2016), with further color-biased regions along the ventral visual pathway (Lafer-Sousa & Conway 2013). Much of what we know about the neural mechanisms of color representation in the visual cortex has been found using electrophysiology or optical imaging in macaques, which are thought to provide a good model of the human color vision system. In the macaque primary visual cortex (V1), the tuning of color-selective neurons is variable and not predominantly along the cardinal axes [S/(L + M) and L/(L + M)] of the retinogeniculate color pathways (Johnson et al. 2004), especially for spatially selective double opponent cells that also respond to luminance (Johnson & Mullen 2016). Such cells may be arranged systematically by hue across the cortical surface (Li et al. 2022, Tanigawa et al. 2010, Xiao et al. 2007). In humans, direct measurements of cortical color mechanisms rely on neuroimaging, which has provided evidence that human color-selective or color-biased regions are similar to those of macaques (Johnson & Mullen 2016, Lafer-Sousa et al. 2016, Mullen 2019), as well as evidence of hue preferences or biases for single voxels (Parkes et al. 2009).

Little to nothing has been reported about individual differences in cortical color mechanisms, and any progress is likely to be a significant challenge with current neuroimaging methods. If interindividual variability is observed in electroencephalographic (EEG) data, then it may be attributable to differences in the sampling of activity in underlying cell populations, rather than to individual differences in the complements of neural mechanisms. For functional magnetic resonance imaging, there are several problems to overcome, including the need to increase sample sizes (Dubois & Adolphs 2016, Elliott et al. 2020), the need to match homologous brain areas across participants with different neuroanatomy (Dubois & Adolphs 2016), the need to account for influences on the BOLD response other than neural activity itself (Dubois & Adolphs 2016), and the need to measure and increase reliability (including for preprocessing) to

avoid attributing measurement noise to individual differences (Dubois & Adolphs 2016, Elliott et al. 2020). A promising avenue for research on individual differences using neuroimaging may be representational similarity analysis, which abstracts representations of a set of stimuli by measuring the correlations between their multivoxel (or multi-electrode or multifrequency in EEG) activity patterns. Using this method, Brouwer & Heeger (2013) have found task-specific categorical representation of hue in VO1—in principle, the same method could be used to investigate individual differences in color representation, whether they are task specific or not.

In the absence of neuroimaging data, psychophysical evidence can be brought to bear on the question of individual differences in cortical color mechanisms. Elliott et al. (2012) adapted participants to modulations of color contrast along either the cardinal axes of the MacLeod Boynton chromaticity diagram, thought to isolate the dominant retinogeniculate color mechanisms, or intermediate axes. Following suggestions in earlier work (Krauskopf et al. 1982, Webster & Mollon 1991), they found individual differences in the degree to which sensitivity loss following adaptation was selective for the adapted color axis. Elliott et al. attributed these differences in the selectivity of adaptation to strongly correlated differences in the overall strength of adaptation (which was influenced by age), but another study found that the selectivity of adaptation shows significant individual differences (test–retest reliability) even when the overall strength of adaptation is accounted for (Lawrance-Owen 2012). In another example, individual differences in judgements of the constituents of color appearance have been used as a tool for understanding cortical color mechanisms (see Section 9): Emery et al. (2017) performed a factor analysis of individual differences in hue-scaling data to reveal seven or more underlying cortical color channels that can be weighted differently in different individuals.

4. INFLUENCE OF THE COLOR ENVIRONMENT

Another factor that may influence individual differences in color perception is long-term adaptation or calibration to the color properties of environments. This could serve either to increase individual differences by providing an additional source of variance if environments differ or to reduce them (Emery & Webster 2019) if calibration to common chromatic features of environments counteracts differences that might be expected to arise from the peripheral and neural factors discussed in Sections 2 and 3 (Emery & Webster 2019, Webster 2015a, Webster et al. 2005). Adaptive gain changes and other forms of adaptation and perceptual learning are expected to tune visual systems to the sensory characteristics of the environments in which they are immersed (Webster 2015b). Such adaptation can occur over short, medium, and long timescales, but it is long-term adaptation or calibration to natural scenes that would cause enduring individual differences in color vision between people living in different visual environments. In support of this possibility, aspects of color vision, such as discrimination (Bosten et al. 2015, Regan et al. 2001), the chromatic contrast response function (MacLeod 2003, MacLeod & von der Twer 2003), the perceptual balance of colors along different axes (McDermott & Webster 2012), unique hue perception (Mollon 2006), and nonlinearities such as the Abney effect (Long et al. 2006), are aligned with the color statistical properties of natural scenes.

Adaptation to the statistics of visual environments can be understood in the framework of efficient coding (Laughlin 1981), which postulates that visual mechanisms efficiently represent information in the natural world. In this framework, the null point or resting level of a visual mechanism encodes the center of the distribution of available stimulus levels, while the contrast response function reflects the cumulative distribution of stimulus contrasts in the environment (Laughlin 1981) such that each level of neural activity reflects an equal step in the representation of information present in natural scenes. For color vision, adaptation may maintain the average

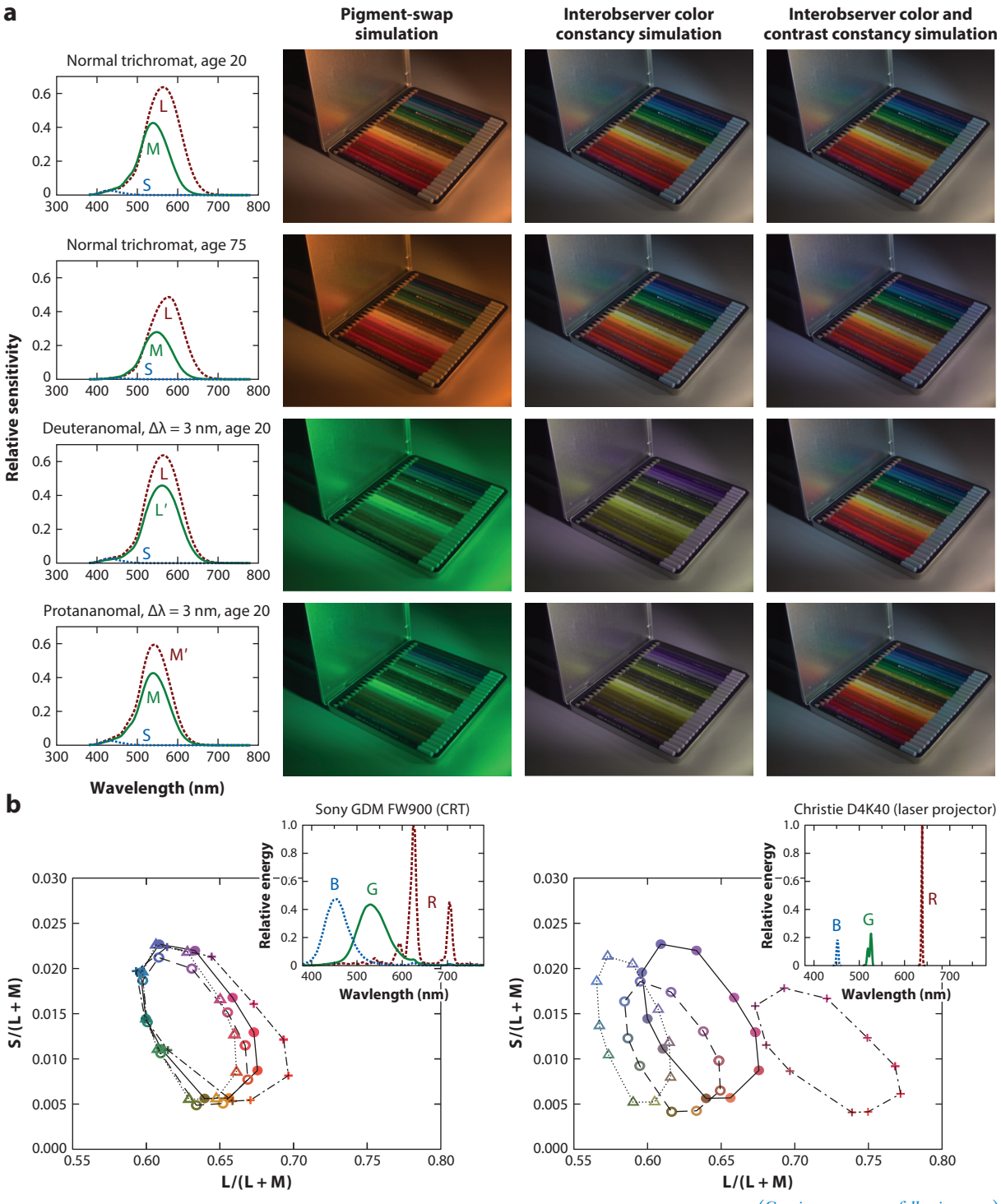
chromaticity present in the environment at the null point of color mechanisms, so that the average chromaticity is perceived as achromatic (Webster et al. 2005). The shape of the chromatic contrast response function for a hue mechanism may reflect the distribution of contrasts of that hue in the environment (MacLeod & von der Twer 2003).

4.1. Interobserver Constancy

The term "interobserver constancy" was coined to describe the effect of adaptation to a common environment compensating for individual differences in the visual system that might otherwise provoke different color percepts, such that perception is normalized across observers (Emery & Webster 2019, Webster et al. 2005). One way in which this could occur is via gain changes in visual mechanisms, where the visual system adapts to the prevailing environmental mean along a stimulus dimension. One good example of interobserver constancy probably achieved by gain changes is the stability of color appearance with age (e.g., as illustrated by the interobserver color constant simulations of color appearance for observers aged 20 and 75 in **Figure 1*a***). While lens brunescence filtering short-wavelength light causes short-wavelength discrimination thresholds to increase substantially with age (Wuerger 2013), little change is observed in color appearance measured using settings of unique hues (Schefrin & Werner 1990, Werner & Schefrin 1993, Wuerger 2013) or color naming (Hardy et al. 2005, Lillo et al. 2012). Similarly, there is evidence that individual differences in macular pigment density are calibrated out by compensatory changes in gain (Stringham et al. 2006). Adaptive gain changes can occur throughout the visual processing hierarchy beginning in the receptors [von Kries 1970 (1902)] and can result from a mixture of short-, medium-, and long-term mechanisms (Webster 2015b). However, there is evidence that the gain changes that maintain stable color appearance during aging result from long-term adaptation. When cataract patients have their cataracts removed, their settings of unique white initially shift rapidly away from short wavelengths (which better reach the retina postsurgery) but return gradually over several months to the presurgery settings (Delahunt et al. 2004).

In addition to interobserver constancy for the mean chromaticity, second-order (contrast) adaptation may maintain interobserver constancy for the distribution of contrasts present in the environment. Anomalous trichromacy provides an interesting natural experiment for this hypothesis (Isherwood et al. 2020). Since the spectral sensitivity functions of the L and M cones overlap to a much greater degree in anomalous trichromacy than in normal trichromacy, the range of comparison ratios between the two cone types is reduced, effectively reducing color contrasts selectively along the anomalous trichromatic equivalent of the L/(L + M) axis. However, postreceptorally, anomalous trichromats should have the same range of neural levels with which to represent this restricted range of stimulus contrasts as normal trichromats have to represent their full range. Making full use of the available neural range would amplify the initially reduced signals; thus, the range of color contrasts represented at later stages of anomalous trichromats' visual systems may be the same as in normal trichromacy (see the inter-observer contrast and constancy simulation in **Figure 1*a***). There is now substantial behavioral evidence that such postreceptoral compensation indeed occurs (Boehm et al. 2014, Lindsey et al. 2021, Regan & Mollon 1997, Vanston et al. 2021), and recent neuroimaging evidence indicates a cortical locus just later than V1 (Tregillus et al. 2021).

Another mechanism of interobserver constancy may be calibration to dominant or salient perceptual features of the environment. For example, it has been suggested that unique hues may be set by familiarity with natural daylights, since the chromaticity of sunlight lies at the mean setting of unique yellow, and the chromaticity of skylight lies at the mean setting of unique blue (Mollon 2006). Anomalous trichromacy also provides a test of this hypothesis, as discussed in Section 8.1.



(Caption appears on following page)

Figure 1 (*Figure appears on preceding page*)

(*a*) Simulations of the appearance of a scene for individuals with different cone sensitivities and prereceptoral filters: a standard normal trichromat aged 20, the same normal trichromat aged 75, a deuteranomalous trichromat with a small (3 nm) spectral separation between the peak sensitivities of two long-wavelength-sensitive cone types, and a protanomalous trichromat with the same small spectral separation between the two medium-wavelength-sensitive cone types. The simulations are based on a hyperspectral image of an object under broadband illumination captured using a calibrated IQ spectral camera (SPECIM, Oulu, Finland). In each case, LMS tristimulus values were calculated for each pixel for each observer using a model of cone fundamentals based on a nomogram by Stockman & Sharpe (2000). Lens and macular pigment prereceptoral filters were added according to Stockman et al. (1999), using an equation relating lens density to age provided by Pokorny et al. (1987). Values for optical density of 0.38 for the L and M cones and 0.3 for the S cones (Stockman et al. 1999) were used. The resulting observer-specific modeled cone fundamentals are shown. Pixelwise observer-specific LMS tristimulus values were then transformed to RGB values for an arbitrary iPad Pro display (Apple, Cupertino, CA) via an LMS-to-RGB transform matrix constructed for the standard normal trichromat. The results, presented in the first column of images (pigment-swap simulation), simulate how the scene would appear to the normal trichromat if they had access to the observer-specific tristimulus values for the other individual observers and if no postreceptoral processes compensated for the differences in cone activities. In the second column (interobserver color constancy simulation), the L, M, and S values have been rescaled so that their means are the same as those elicited by standard illuminant D65 for the standard normal trichromat. This transformation models von Kries [1970 (1902)] adaptation and provides interobserver constancy, since mean cone activities are equalized across observers. In the third column (interobserver color and contrast constancy simulation), a model of postreceptoral compensation for observer-specific differences in color contrast has been additionally applied by restoring the L/(L + M) and S/(L + M) contrasts available to the standard normal trichromat to the contrasts along the equivalent axes for the other observers (Webster et al. 2010). The simulations show how interobserver color and contrast constancy have the potential to largely normalize color appearance across observers with different peripheral visual systems. (*b*) Illustration of the effect of observer metamerism for the same observers for two different displays. Plotted for each observer are the chromaticities [in a version of the MacLeod & Boynton (1979) chromaticity diagram] of RGB metamers for a set of Munsell color surfaces (various hues of Chroma 6 and Value 6) under a D65 standard illuminant. For the traditional CRT display with relatively broadband primaries (spectra are presented as an insert), interobserver agreement is quite good. Interobserver agreement is much poorer for the laser projector, where the chromaticities that are metameric with the Munsell surfaces do not overlap at all for the protanomalous observer and the other observers. Abbreviations: B, blue; CRT, cathode-ray tube; G, green; L, long; M, medium; R, red; S, short.

4.2. Adaptation to Different Color Environments

The same adaptive processes that maintain interobserver constancy would create individual differences in color perception for observers living in different visual environments. There is substantial variation in color statistics among geographic locations (Juricevic & Webster 2009), likely caused by variation in vegetation, terrain, relief, altitude, climate, the presence or absence of bodies of open water, urbanization, and culture-specific architecture. There can also be substantial variation across seasons at a constant geographic location (Juricevic & Webster 2009, Webster et al. 2007) caused by changes in weather, natural and artificial illumination, and vegetation (Granzier & Valsecchi 2014, Webler et al. 2019, Webster et al. 2007). There have been only a few attempts to relate differences in color vision among observers at different geographic locations to differences in environmental color statistics. Webster et al. (2002) found differences in unique yellow between people living in India and people living in the United States that could not be obviously related to differences in the color statistics of the local environments. A recent study by Josserand et al. (2021) revealed that some of the variance in color naming for blue and green can be accounted for by proximity to bodies of water.

Investigating the impact of seasonal variation, rather than variation among geographical locations, offers the ability to target within-individual effects to increase power (by factoring out other sources of individual variability) and to avoid potential confounds such as genetic or physiological differences among populations. Indeed, several existing studies of seasonal variation in color vision have produced promising results. Laeng et al. (2007) found an interaction between season of birth and latitude on color discrimination: People born in the autumn within the Arctic Circle made more errors on the Farnsworth-Munsell (FM 100) hue test than those born outside of it, with the opposite pattern for people born in the summer. Since the effect was measured in adulthood,

the result implies that early exposure to particular illuminants present in different seasons has a long-term effect on color vision. Results by Welbourne et al. (2015) show that seasonal variation in color perception is also possible in adulthood: They found a significant effect of season on settings of unique yellow (although not on unique green or Rayleigh matches).

5. COLOR MATCHING AND OBSERVER-SPECIFIC COLOR SYSTEMS

The phenomenon of observer metamerism means that, if two different spectral power distributions match for one observer (a metameric match), then they will necessarily not match for a different observer with a different set of cone spectral sensitivities or ocular filters. Although color spaces are constructed to predict color matches and color appearance (Fairchild 2019), the standard observer models based on average sets of cone fundamentals or color matching functions that underlie the spaces will not accurately predict color matches or color appearance for any particular observer. However, models incorporating variation in cone spectral sensitivities and ocular filtering can provide an estimate of the range of individual differences expected for stimuli constructed from any set of primaries. Several formal models have recently been developed, including an extension of CIE 2006 to incorporate interobserver variation (Asano et al. 2016a) and a system that transforms chromaticities from an observer-specific color space to a standard color space using smooth metamers (Smet et al. 2021).

Between-observer metameric mismatches can be quite large. **Figure 1*b*** shows the RGB colors needed to match physical colored surfaces for different observers. Even for traditional displays with relatively broadband primaries, different observers require visibly different RGBs to match the surfaces, but disagreement increases as the spectral bandwidth of the display primaries reduces (Asano et al. 2016b, Yuan et al. 2021) and is also affected by the wavelengths of the peaks in the display primary spectra (Li et al. 2021).

Displays are typically calibrated to reproduce colors in the natural world for a standard observer, although there are efforts to better accommodate individual differences (Canham et al. 2020, Morvan et al. 2011, Whitehead et al. 2021, Zhou et al. 2017). However, even for standard displays, observers with very different visual apparatus to the standard observer do not typically object to the colors rendered. Most likely some compensation for mismatched colors is achieved via short-term adaptation, but observers may also have a relatively high tolerance for color mismatches with spectra in the external world. The limits of adaptation or tolerance will determine the need for observer-specific display calibration, especially as display technologies increase their color gamuts by narrowing the spectra of the primaries.

6. INDIVIDUAL DIFFERENCES IN COLOR DISCRIMINATION

Variations in receptor sensitivities or prereceptoral filtering cause individual differences in the ability to discriminate colors. On average (as expected), observers of different classes (normal trichromats, anomalous trichromats, and dichromats) differ in their abilities to discriminate colors (Barbur et al. 2008, Bento-Torres et al. 2016, Rodriguez-Carmona et al. 2012, Shinomori et al. 2016). However, there is overlap in discrimination performance among groups. For example, some red–green dichromats have better red–green color discrimination for large fields than do extreme anomalous trichromats. Mysteriously, some anomalous trichromats have color discrimination that is average or better than average for normal trichromats. Such minimalanomales (Jordan & Mollon 2019) or pigmentfarben anomales (Verriest et al. 1982) may read pseudoisochromatic plates designed to detect red–green CVD without error and may be detected only by their anomalous Rayleigh matches.

The existence of group differences in red–green color discrimination is not surprising. Any variation that reduces the sizes of cone opponent signals is expected to reduce color sensitivity. More surprising are cases such as that of pigmentfarben anomales where the coupling between modeled cone opponent signals and color discrimination is not as tight as predicted. Among anomalous trichromats, there is substantial individual variability in the degree to which the two medium- or long-wavelength-sensitive cone types overlap in their spectral sensitivities. The greater the spectral overlap, the smaller the difference signal carried by the L versus M (midget) cone opponent system is predicted to be. However, the correlation between the spectral separation of the two cone sensitivity functions (estimated from genotype) and color discrimination accounts for only approximately 15% of the variance in red–green color discrimination thresholds (for a meta-analysis, see Bosten 2019). Similarly, macular pigment density accounts for only approximately 20% of the observed variance in thresholds for the intensity of short-wavelength light (Davison et al. 2011), does not seem to be correlated with tritan thresholds (Rodriguez-Carmona et al. 2006), and does not seem to impact performance on tests of hue discrimination (Davison et al. 2011). Another phenomenon that is not well accounted for by models of color vision based on signals from two receptor types is the residual red–green color discrimination shown by dichromats, particularly for large fields (Breton & Tansley 1985, Crognale et al. 1999, Scheibner & Boynton 1968, Smith & Pokorny 1977).

Loosening the relationship between red–green color discrimination and the cone opponent signals predicted from cone spectral sensitivities and prereceptoral filtering may be other factors that are also expected to contribute to individual differences among normal trichromats (Bosten et al. 2014, Fernandes et al. 2020, Hasrod & Rubin 2019). One likely factor is contributions to color signals from additional receptor types. Some dichromats who can make trichromatic color discriminations for large fields may have some residual cones of the missing class in the retinal periphery, but genotyping has shown that at least some such dichromats do not have residual cones (Crognale et al. 1999, Sanocki et al. 1997). Another possible contributor to individual differences is intrusion by melanopsin-containing ganglion cells (Isherwood et al. 2020). Similarly, the rods may contribute to color vision, especially in mesopic conditions (although they do not provide the sole explanation for large-field trichromacy; see Breton & Cowan 1981, Crognale et al. 1999, Nagy 1980). There may also be useable signals from S cones in medium- and long-wavelength spectral regions at sufficiently high intensities (McMahon & MacLeod 1998). Other potential sources of variance in color signals that have been proposed but not tested in humans include differences in optical density between cone types or among subsets of cones expressing the same photopigment (He & Shevell 1995, Sanocki et al. 1997, Thomas et al. 2011), individual differences in the ability to make color comparisons between center and periphery in the presence and absence of macular pigment (Broackes 2010b), and individual differences in the ability to use signals from chromatic aberration (Forte et al. 2006, Stubbs & Stubbs 2016).

Another factor known to influence individual differences in color sensitivity is age. Color discrimination thresholds reduce rapidly over the first few years of life and continue to reduce into young adulthood, whereafter they slowly increase into old age (Barbur & Rodriguez-Carmona 2016, Kinnear & Sahraie 2002, Knoblauch et al. 2001, Paramei & Oakley 2014, Shinomori et al. 2016). Lens brunescence accounts for much of the effect of aging (Schefrin et al. 1992, Shinomori et al. 2016) but is not the sole determinant of sensitivity changes even for short-wavelength light: When stimuli are equated for retinal illuminance across observers, an age-related decline in S-cone sensitivity is still observed (Schefrin et al. 1995). The remaining effect of aging on discrimination of S-cone stimuli acts on absolute thresholds rather than the Weber fraction (although, interestingly, aging does affect Weber fractions for color discrimination that relies on L versus M;

Shinomori et al. 2001) and could be attributable to increasing neural noise or a reduction in the efficiency of light adaptation (Schefrin et al. 1995).

There must be many additional visual and cognitive factors that contribute to individual differences in color discrimination thresholds. Some have been investigated, e.g., pupil size (Bosten et al. 2014), iris color (Bosten et al. 2014, Zlatkova et al. 2014), and sex (Rodriguez-Carmona et al. 2008). Importantly, contributing factors may not be independent; e.g., iris color is correlated with macular pigment density, and pupil size may be correlated with iris color and sex, meaning that care is needed to disentangle independent effects on color discrimination (e.g., Dain et al. 2004). The factors discussed in this review are expected to affect the size or availability of color signals, but variation in neural noise likely also plays a role, as it does for achromatic contrast sensitivity (Vilidaite & Baker 2017). Cognitive factors such as attention and motivation have not been investigated for color discrimination but probably influence thresholds, as they do in other stimulus domains (Carrasco 2006, Zacharopoulos et al. 2014). Lastly, long-term calibration of individual color vision systems to different chromatic environments may also influence individual differences in color discrimination (see Section 4).

7. INDIVIDUAL DIFFERENCES IN COLOR CONSTANCY AND ADAPTATION

Perception is color constant, in that the perceived colors of objects remain roughly stable despite (often large) changes in the spectral power distributions of light reflected under different illuminants. However, there is substantial variation within and between studies in color constancy indices describing the extent to which observers are color constant, attributable to the different methods used and to individual differences (Hurlbert 2021, Olkkonen & Ekroll 2016). Some of the observed variation between individuals may be attributable to differences in task strategy (the instructions in color constancy tasks are often imprecise and open to interpretation). This hypothesis is rendered plausible by findings that show that manipulating task strategy by changing instructions can result in large differences in color constancy indices (Arend & Reeves 1986, Radonjić & Brainard 2016). However, individual differences in color constancy indices occur even within an instruction condition (Radonjić & Brainard 2016).

Currently, the majority of research on individual differences in color constancy is restricted to one surprising stimulus. In early 2015, when vision scientists first saw the infamous image of #theDress spreading virally on social media, they collectively thought, "Why is everyone suddenly getting excited about color constancy?" However, rather than color constancy causing the huge stir (which would have been fantastic too), it was individual differences. The apparent differences in how different individuals perceive the dress are very striking, with some describing it as white and gold and others as blue and black. Since the image briefly dominated internet traffic, there have been several investigations of the individual differences involved, as well as a special issue in *Current Biology* (see Brainard & Hurlbert 2015). A variety of (not necessarily independent) low- and high-level factors have been uncovered that are correlated with perception of the dress, including age (presumably via lens density or S-cone sensitivity) (Aston & Hurlbert 2017, González-Martín-Moro et al. 2021, Lafer-Sousa et al. 2015), macular pigment density (Rabin et al. 2016), genetic and environmental factors (Mahroo et al. 2017), gender (Lafer-Sousa et al. 2015), one-shot learning (Daoudi et al. 2017), pupil diameter (Vemuri et al. 2016), achromatic settings (Feitosa-Santana et al. 2018), activity patterns in frontal and parietal brain regions (Schlaffke et al. 2015), asymmetries in perception of or neural responses to blue and yellow (Retter et al. 2020, Winkler et al. 2015), and circadian rhythms (Lafer-Sousa & Conway 2017). Overall, the different categories of color perception for the image seem to stem from variations in interpretation of the illuminant (Murray & Adams 2019, Witzel et al. 2017): Observers who name the dress blue

and black tend to perceive it as more brightly illuminated by a warmer illuminant, whereas those describing it as white and gold tend to perceive it as dimly illuminated by shadowy bluish light (Lafer-Sousa & Conway 2017, Toscani et al. 2017, Wallisch 2017). The other factors that have been found to correlate with the individual differences presumably affect perception by influencing either prior assumptions or incoming sensory evidence for the dress's illumination (Brainard & Hurlbert 2015).

8. CONSEQUENCES FOR COLOR APPEARANCE

The above sections have touched on individual differences in color appearance that may result from the relatively well-defined variations in cone spectral sensitivities or ocular filtering, from less well-characterized variations in retinogeniculate or cortical color mechanisms, or from processes of adaptation of color constancy. In this section, I review evidence related to how color appearance varies between individuals and the causes of the variation.

8.1. Unique Hues

Because they provide anchor points in the perception of color, the stimuli for which individual differences have been most studied are the so-called unique hues, subjectively pure red, blue, yellow, green, and white. There is surprisingly large variability in settings of unique hues (Hinks et al. 2007; Kuehni 2001, 2004; Schefrin & Werner 1990; Webster et al. 2000b; Wuerger et al. 2005), and between 27% (for blue) and 60% (for red) of this variability is shared between two sessions, implying stable individual differences (Bosten & Lawrance-Owen 2014). It is a reasonable supposition that differences in cone sensitivity functions, differences in prereceptoral filtering, or other differences in the peripheral color vision system should affect the perception of unique hues, yet correlations between unique hue settings and these factors [with the notable exceptions of relationships between unique green and iris color (Jordan & Mollon 1995) and unique green and age (Wuerger 2013)] have mostly proven elusive (Brainard et al. 2000, Jordan & Mollon 1995, Miyahara et al. 1998, Neitz et al. 2002, Pokorny & Smith 1977, Volbrecht et al. 2000). Likewise, attempts to relate differences in unique hues to differences in color sensitivity or in the positions of the cone opponent axes have also produced negative results (Webster et al. 2000b).

A lack of evidence for a neural color representation based on unique hues (Bosten & Boehm 2014, Valberg 2001) has led to the proposal that unique hues are instead associated with particular spectra in the environment (Philipona & O'Regan 2006, Witzel et al. 2015), such as natural daylights (Mollon 2006). Individual differences can be used to test such hypotheses: As Jordan & Mollon (1995) have argued, if different observers with different peripheral visual systems agree that particular spectra in the natural environment, e.g., sunlight or skylight, are unique, then they will predictably disagree on the laboratory stimuli (monochromatic lights or mixtures of display primaries) required to match the natural spectra. **Figure 2** shows that different settings of unique yellow for normal and deuteranomalous trichromats (Lindsey et al. 2021) occur at predicted match points with natural daylights, bolstering the idea that unique hues arise from experience with natural illuminants (Mollon 2006). However, the existence of only a moderately smaller range of individual differences for broadband stimuli (that presumably better approximate natural spectra) than for narrowband stimuli (Hinks et al. 2007; Kuehni 2001, 2004; Webster et al. 2002) remains problematic for this theory.

8.2. Color Similarity

Methods involving dissimilarity judgements allow the color appearance relationships among the members of an arbitrary set of stimuli to be characterized. A particularly fruitful method for the

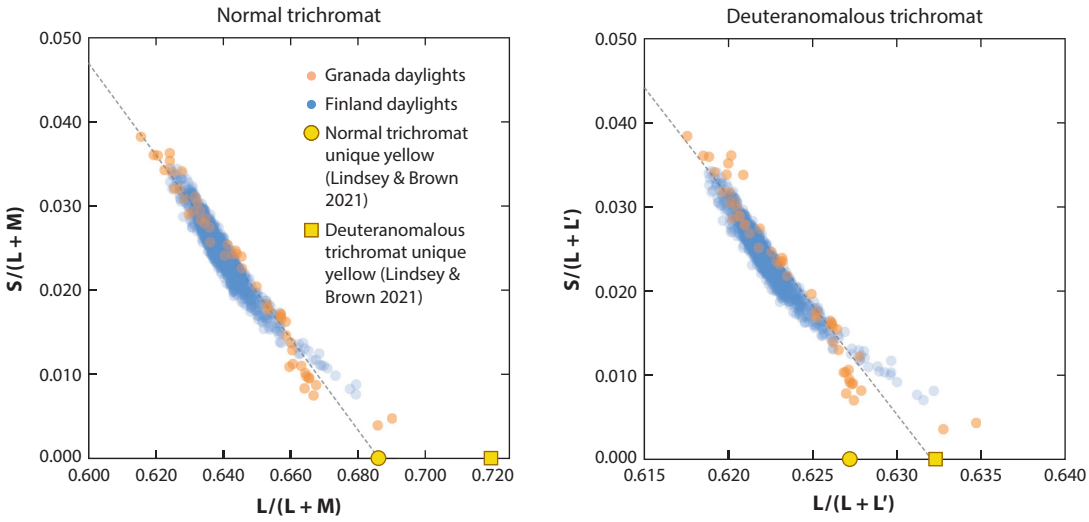


Figure 2

Natural daylights predict monochromatic unique yellow for normal trichromats and anomalous trichromats. The chromaticities of natural daylights measured in Granada (*orange*) (Hernández-Andrés et al. 2001) and Finland (*blue*) (Kohonen et al. 2006) and a linear fit through the distributions of daylight chromaticities (*dashed lines*) are shown in versions of the MacLeod & Boynton (1979) chromaticity diagram constructed for normal (*left*) and deuteranomalous (*right*) trichromats, based on the Smith & Pokorny (1975) cone fundamentals for normal trichromats and the DeMarco et al. (1992) cone fundamentals for anomalous trichromats. If unique yellow is related to natural daylights, then unique yellow for monochromatic lights should occur at the intersection of the daylight axis (the best-fitting line through natural daylights) and the spectrum locus of monochromatic lights. For normal trichromats, the line through natural daylights intersects the spectrum locus at 575 nm; for deuteranomalous trichromats, this intersection occurs at 583 nm. The wavelengths of intersection for both groups accord with recent measurements by Lindsey & Brown (2021), who found unique yellow to be located at 575.3 nm for normal trichromats (*yellow circles*) and at 582.7 nm for deuteranomalous trichromats (*yellow squares*) (for a summary of deuteranomalous settings of unique yellow from other studies, see Lindsey et al. 2021). The results indicate that individual differences in unique yellow for monochromatic lights can be predicted as an interaction between experience with natural daylights in the external environment and observer-specific visual apparatus (Jordan & Mollon 1995, Mollon 2006).

analysis of perceived color dissimilarities has been multidimensional scaling (MDS), which finds the locations of stimuli in a coordinate space that minimizes the difference between stimulus proximities in the derived space and an input matrix of pairwise dissimilarity ratings (Shepard 1962). Perceptual color spaces reconstructed in this way resemble stimulus color spaces; e.g., in a 2D MDS solution, hue tends to vary tangentially, and saturation tends to vary radially. Luminance may vary along a third dimension (Indow 1980). MDS has been used to investigate group differences in color appearance. Typically, for a set of roughly isoluminant colored stimuli, trichromats show a 2D perceptual color space, while dichromats show a single color dimension (Paramei & Cavonius 1999, Paramei et al. 1991). Anomalous trichromats show a 2D MDS solution that is somewhat contracted along the color dimension that relies on cones sensitive to long and medium wavelengths (Boehm et al. 2014, Paramei & Cavonius 1999, Paramei et al. 2001), although not to the extent predicted from the increased spectral overlap of their cones (Boehm et al. 2014; see Section 4.1). However, for particular stimulus sets designed to be metameric for normal trichromats, anomalous trichromats may show a 2D solution where normal trichromats show a 1D solution (Bosten et al. 2005, Jordan et al. 2010). Heterozygote carriers of protan or deutan deficiency may show a mild contraction of MDS-reconstructed color spaces along the red–green axis (Bimler & Kirkland 2009). However, for stimuli that are metameric for the normal trichromat, some carriers

of anomalous trichromacy can show a color dimension that is accessible to anomalous trichromats but not normal trichromats (Jordan et al. 2010; see Section 2.6).

Small sex differences have been found: One study reported that men place less weight on a red–green axis and more on a luminance axis than do women (Bimler et al. 2004), although this has not been replicated in a different population (Bonnardel et al. 2016). A later study showed subtler effects of gender on the spacings of stimuli in particular regions of color space (Bimler & Bonnardel 2018). Individual differences in color appearance among normal trichromats have also been investigated using MDS: There are small but reliable differences in the weightings of different stimulus dimensions in judgements of color dissimilarity (Bonnardel et al. 2016). A study on the MDS-reconstructed color spaces of normal trichromat MZ and dizygotic (DZ) twins revealed higher concordance in MZ than in DZ twins, suggesting that individual differences in perceptual color spaces are heritable (Paramei et al. 2004).

8.3. Color Naming

A wealth of studies have drawn on several large data sets (Berlin & Kay 1969, Jameson 2018, Kay et al. 2010, MacLaury 1997) to reveal huge variety but also surprising consistency among color lexicons around the world (for a recent review, see Lindsey & Brown 2021). Most research has emphasized commonalities in color category centroids and focal colors across languages (Kay & Regier 2003, Regier et al. 2005), favoring a universalist perspective. A minority of research has pointed to language-specific idiosyncrasies (Paramei 2005, Roberson 2005), favoring a relativist view, where convergent evolution of social and perceptual demands shape the cross-linguistic commonalities observed (Gibson et al. 2017; Jameson 2005, 2010; Zaslavsky et al. 2018). More seldom discussed are the substantial individual differences in color naming that occur within a culture or among speakers of the same language (Jameson 2005, 2010; Lindsey & Brown 2009, 2016; Webster & Kay 2005, 2007). Surprisingly, individuals within a language form clusters in their color naming systems that are similar to the clusters of naming systems that exist between languages (Lindsey & Brown 2009). Whether these commonalities stem from biological differences between subgroups or the presence of common subcultures (that could, e.g., expose subgroups to characteristic patterns of environmental stimuli) remains to be determined (Lindsey & Brown 2009, 2016; Webster & Kay 2007).

In addition to an effect of individual differences in color perception on color terminology, there could be an effect in the opposite direction, known as the Whorf hypothesis (Regier & Kay 2009): Differences in language could cause differences in color discrimination or appearance. A relatively well-studied example is the case of the Russian blues (Paramei 2005): Some languages split the category of blue with two basic terms (in Russian, goluboy for light blue and siniy for dark blue). A report by Winawer et al. (2007) of faster reaction times for color discrimination across the boundary of blue terms for Russian than for English speakers was followed by evidence of language-specific differences in event-related potentials (ERPs) at the category boundary (Thierry et al. 2009). However, Martinovic et al. (2020) found no such effects in ERPs, and differences in discrimination thresholds at category boundaries, which would more securely imply an effect of language on perception rather than response, have not been found (Roberson et al. 2009, Witzel & Gegenfurtner 2013).

8.4. Subjective Color Experience

The philosophical thought experiment of spectrum inversion proposes that subjective experiences of color may be inverted or otherwise discordant between individuals (for a recent discussion, see Ross 2021). In the absence of a neurophysiological marker of phenomenal experiences of color,

the proposition may be impossible to address. However, what we already understand about individual differences in the apparatus for color vision and their perceptual consequences allows us to conclude that subjective experiences triggered by lights or surfaces in the external world must vary between individuals. If two different spectra match for one individual, then, due to observer metamerism, they would be mismatched for a second individual with different visual apparatus. Since the color experiences elicited by the two spectra are equal for the first individual, one or both of the colors experienced by the second individual must differ from those experienced by the first. In some cases, color experiences elicited by the same stimuli may be sufficiently different in two individuals to prompt different color terms. The set of stimuli used by Bosten et al. (2005) to investigate anomalous color vision appeared to normal trichromats to contain variations on khaki green. One such normal trichromat expressed surprise when she witnessed her deuteranomalous partner swiftly separate them into two groups and call one group red and the other green.

While observer metamerism allows us to infer that subjective experiences of color differ between observers, it does not tell us how they differ. However, one source of evidence for how neural hardware constrains color experience may be offered by cases where color vision differs between the two eyes. Colors presented to the tritanopic eye in two people with unilateral tritanopia have been matched using the normal trichromatic eye along curved loci in trichromatic color space between red and blue (Alpern et al. 1983a,b) and between bluish green and orange (Graham et al. 1967). In unilateral deuteranopia and protanopia, colors viewed using the dichromatic eye may also be matched to colors along curved loci (Broackes 2010a). Such cases are rare and may differ in important respects from cases of bilateral dichromacy (e.g., the presence of the trichromatic eye could influence the way in which the brain learns to process color); nonetheless, the existence of these cases casts doubt on the assumption applied in models of dichromatic color appearance that colors vary linearly between the two poles of the normal trichromatic axis that is retained (e.g., as in **Figure 1**). In addressing this issue, studies of color experience in the first human recipients of gene therapy for dichromacy will be instructive (for a study in adult squirrel monkeys, see Mancuso et al. 2009).

9. INDIVIDUAL DIFFERENCES AS A TOOL FOR COLOR SCIENCE

As well as being of interest in their own right, individual differences can serve as a tool for understanding the mechanisms of perception (Mollon et al. 2017, Wilmer 2008). Since variability in data has historically typically been ignored in favor of analyzing means, there is untapped potential in existing data sets for analysis of individual differences to provide new insights. In designing new research aiming to exploit individual differences as primary or secondary measures of interest, researchers will need, especially in psychophysics and neuroimaging, to include larger samples than are currently typical. They must also deal with challenges such as the need to target individual differences in perception itself, rather than differences in nonvisual factors such as motivation, task strategy, or response bias, and the need to ensure that variance due to various sources of measurement error is not incorrectly attributed to individual differences of interest (Mollon et al. 2017, Olkkonen & Ekroll 2016, Wilmer 2008).

That said, there are several ways in which to apply the tool of individual differences in research on color perception. First, individual differences may constrain the space of possible underlying variables. A classic example was König & Dieterici's (1892) derivation of cone sensitivity functions from the different color matches of normal trichromats and dichromats. Trichromatic cone fundamentals must be among an infinite number of linear transformations of color matching functions, but to identify the correct transformation, constraints are needed. Simpler dichromatic color matching functions provided one of the constraints: König & Dieterici correctly assumed that dichromats and trichromats share two of the three normal trichromatic cone fundamentals.

Second, correlational studies may be used to connect accounts of color vision at different levels. Variation at genetic, brain structural, neurochemical, behavioral, and cultural levels may be connected by correlation across individuals, contributing a complete description of the mechanisms of a trait at all of its levels of explanation. A good example comes from work connecting the absence of separate color names for green and blue to high lens density via exposure to UV-B light (Josserand et al. 2021, Lindsey & Brown 2002). Genome-wide association is a promising method for discovering genetic influences on color perception other than those caused by the relatively well-known variations in the L and M opsin gene array. To date, this method has been underutilized and largely restricted to clinical research, although some new candidate genes have emerged, including 139 loci for macular thickness (distinct from, but related to, macular pigment density) (Gao et al. 2019), *RXRG* for L:M cone ratio (Lawrance-Owen et al. 2014), and several candidates suggestively associated with sensitivity to S-cone-isolating stimuli (Bosten et al. 2014). There is similar untapped potential for correlational studies between perceptual traits and structural or functional neuroimaging (or retinal imaging) measures (for a review, see Gu & Kanai 2014).

Third, statistical techniques for dimension reduction in data sets may be used to identify underlying variables that affect a collection of different observed behavioral (or neuroimaging) traits, measured across individuals (Mollon et al. 2017, Peterzell 2016). Factor analysis of the correlations among the settings of different individuals on measures of color perception have been used to probe the underlying mechanisms. An excellent example of work analyzing existing valuable data sets for individual differences is MacLeod & Webster's (1983) factor analysis of the Stiles-Burch color matching data, which attributed individual differences to variation in macular pigment density, lens density, the spectral positions of the three photopigments, the densities of the three photopigments, and rod intrusion. More recently, factor analysis has been applied to hue-scaling data (Emery et al. 2017) and data from steady-state visually evoked potentials (Kaneko et al. 2021) to estimate the number and tuning of cortical color mechanisms, and to flicker electroretinographic data from mice to estimate underlying cone fundamentals (Peterzell & Crognale 2016).

10. CONCLUSIONS

It is fair to say that our current understanding of individual differences in color vision is patchy. In some cases, we have impressively advanced characterizations of individual differences, certainly in comparison to those available for other visual domains, but in other cases, research has barely begun. In relation to individual differences in the apparatus for color vision, we have a detailed account of variation at the receptor level, particularly of genetic variations affecting the L and M cones, but we lack an understanding of individual differences in postreceptoral and cortical color mechanisms. Individual differences in color matching, discrimination, and appearance have been described, although substantial gaps remain. However, while individual differences in color matching are understood to result from predictable differences in receptor responses, our understanding of the determinants of individual differences in color discrimination and particularly in color appearance is very incomplete. Individual differences in color constancy and contextual effects remain largely unexplored, although research has recently received a boost from the fortuitous discovery of #theDress.

The effects of visual environments on individual differences in color perception are complex: Calibration to common environmental features can reduce individual differences, but calibration to different features is expected to increase them. Using strong theoretical frameworks such as efficient coding, progress has been made, particularly on understanding the effect of calibration to a common environment. However, far more work is needed, both to test the hypothesis that calibration can account for the absence of effects on color appearance that would otherwise be expected from other sources, and to understand the individual differences caused by calibration to

different visual environments. In this endeavor, studies will be needed that measure and account for multiple interacting variables, as in a recent example by Josserand et al. (2021), who measured the impacts of culture, some color statistics of the environment, and different factors influencing exposure to UV light on the presence or absence of separate color categories for blue and green.

A complete explanation of any perceptual process must account for individual differences as well as the population mean. In measuring and attempting to explain the mean only, we may be studying something that has no real existence. Similarly, any successful theoretical framework must account for individual differences. For instance, can Bayesian models of color perception (Brainard 2009) account for individual variability as different distributions of the prior or likelihood? Can efficient coding models account for individual differences by considering either differences in the available neural signals or differences in the distributions of color stimuli across environments? Crucial in their own right to a complete and accurate account of color vision, individual differences also provide a tool to probe the mechanisms of color perception and to address wider theoretical questions. If methods for data dimension reduction for data that include individual differences were to become a more common part of vision researchers' toolkits, both existing and new data sets could be more fully exploited for the insights that they offer.

Understanding diversity in color perception also has implications beyond the field of color science, raising interesting questions in ecology, evolution, anthropology, and philosophy. Prioritization of information in the external world that is important for survival may lead to commonalities across observers in calibrated perception to common environmental features, and how mechanisms evolve that allow perceptual systems to adapt to environments is an important question. It is also possible that there are different perceptual niches available that favor different perceptual strategies, as is thought to occur in other primate species (Osorio et al. 2004, Veilleux et al. 2021). For example, we do not know why anomalous trichromacy is maintained in the population as a significant minority phenotype. Perhaps it is selectively neutral, but it is also possible (as has been suggested; see, e.g., Bosten et al. 2005) that anomalous trichromats have an advantage in spatial vision or in breaking color camouflage; it is also possible that the advantage is possessed by heterozygotes who may have tetrachromatic vision.

Understanding individual differences nuances our conception of the purpose of perception and what it achieves. If two individuals differ in their percepts, then perception is not a case of faithfully mapping the external world to represent an objective physical reality, but rather is a selective take on physical reality. The observer's distinct perceptual experience depends on an interaction between their unique perceptual apparatus and their unique environment. Dalton argued that our propensity to think and talk about the objective properties of the physical world, rather than our perceptual interpretations of them, leads us to ignore individual differences, locking us into incorrect assumptions about perception. Although vision science has now uncovered some of the rich diversity in color perception that was hidden in Dalton's time, much remains to be discovered.

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