Variations in normal color vision. VI. Factors underlying individual differences in hue scaling and their implications for models of color appearance

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Abstract

Observers with normal color vision vary widely in their judgments of color appearance, such as the specific spectral stimuli they perceive as pure or unique hues. We examined the basis of these individual differences by using factor analysis to examine the variations in hue-scaling functions from both new and previously published data. Observers reported the perceived proportion of red, green, blue or yellow in chromatic stimuli sampling angles at fixed intervals within the LM and S cone-opponent plane. These proportions were converted to hue angles in a perceptual-opponent space defined by red vs. green and blue vs. yellow axes. Factors were then extracted from the correlation matrix using PCA and Varimax rotation. These analyses revealed that inter-observer differences depend on seven or more narrowly-tuned factors. Moreover, although the task required observers to decompose the stimuli into four primary colors, there was no evidence for factors corresponding to these four primaries, or for opponent relationships between primaries. Perceptions of “redness” in orange, red, and purple, for instance, involved separate factors rather than one shared process for red. This pattern was compared to factor analyses of Monte Carlo simulations of the individual differences in scaling predicted by variations in standard opponent mechanisms, such as their spectral tuning or relative sensitivity. The observed factor pattern is inconsistent with these models and thus with conventional accounts of color appearance based on the Hering primaries. Instead, our analysis points to a perceptual representation of color in terms of multiple mechanisms or decision rules that each influence the perception of only a relatively narrow range of hues, potentially consistent with a population code for color suggested by cortical physiology.

1. Introduction

Conventional explanations of human color vision are dominated by two fundamental theories. One describes the initial absorption of light by the three classes of cones (trichromacy), and the second the subsequent processing of the cone signals within opponent mechanisms that represent color in terms of red-green, blue-yellow, and black-white dimensions (opponent processing) [e.g. Hurvich and Jameson (1957)]. The spectral sensitivities of the opponent processes were first characterized by hue-cancellation experiments, in which the intensity of a fixed primary hue (e.g. red) was added to null the opponent color (e.g. green) in the stimulus (Hurvich & Jameson, 1955). Subsequently, Jameson and Hurvich also developed a hue-scaling task, in which observers directly judged the strength of the chromatic responses by reporting the proportion of each primary in the stimulus (e.g. the proportion of red and yellow perceived in an orange hue) (Jameson & Hurvich, 1959). Both techniques supported many of the basic premises of opponent-process theory (Hering, 1964): that all hues can be described as a combination of two of the four hue primaries; that red and green, and blue and yellow, are mutually exclusive sensations; and that the four Hering primaries appear pure or unique in that they cannot as easily be perceived as a mixture of other hues (e.g. seeing red as a combination of orange and purple). Both cancellation and hue-scaling experiments have also been widely used to quantify the opponent processes under a variety of conditions, including how color varies with the parameters of the stimulus [e.g. Abramov and Gordon (2005), Abramov,
Gordon, and Chan (1991), Jameson and Hurvich (1956)] or as a function of eccentricity [e.g. Boynton, Schafe, and Neun (1964), Hibino (1992)]. The spectral sensitivities of the red-green and blue-yellow processes can be modeled in terms of the cone sensitivities, thus showing how the cone signals are combined to form the opponent channels (De Valois & De Valois, 1993; Wooten & Werner, 1979; Wuerger, Atkinson, & Crops, 2005). Such analyses led to a standard two-stage model of color vision [e.g. Hurvich and Jameson (1957)] where hue percepts arise directly from the responses in the underlying red-green and blue-yellow mechanisms.

However, while this scheme remains a dominant account of color perception, the neural substrate predicted by opponent-process theory remains elusive. The spectral sensitivities of the primary cell types in the retina and geniculate do not have the tuning required to account for the stimuli that appear unique or pure (De Valois, Abramov, & Jacobs, 1966; Derrington, Krauskopf, & Lennie, 1984). Moreover, color tuning in the visual cortex appears too variable to be consistent with only two discrete chromatic dimensions (Kuriki, Sun, Ueno, Tanaka, & Cheng, 2015; Lennie, Krauskopf, & Sclar, 1990; Shapley & Hawken, 2011; Xiao, Wang, & Felleman, 2003; Zaidi, Marshall, Thoen, & Conway, 2014). Such results have led to suggestions that cells with the appropriate responses may arise later in the system and that chromatic representations undergo transformations at multiple stages, with the neural organization mediating color appearance arising at later stages (Brouwer & Heeger, 2009; De Valois & De Valois, 1993). It has also led to proposals that color percepts may be mediated by specialized neural pathways that arise as early as the retina (Schmidt, Neitz, & Neitz, 2014). The failure to find a clear neural basis for red-green and blue-yellow responses has also raised the possibility that these percepts do not reflect special states in the brain but rather special characteristics of the environment. For example, the blue-yellow axis falls close to the daylight locus, and thus might correspond to a learned property of the world (Lee, 1990; Mollon, 2006; Panorgias, Kulikowski, Parry, McKeefry, & Murray, 2012; Shepard, 1992). By this account, the perceptual null implied by unique hues need not reflect a null in the corresponding neural response, for the percept could in principle be tied to an arbitrary pattern of neural activity (Mollon & Jordan, 1997). However, many still hold that the phenomenal experience of color revealed by tasks like hue scaling ultimately depends on neural processes that directly signal pure hue sensations, and that these processes signal only a small number of sensations corresponding to red-green and blue-yellow qualia.

In the present study we explored the mechanisms of color appearance by analyzing individual differences in hue-scaling functions, using the methods of factor analysis to extract the underlying dimensions of variation in hue-scaling judgments. Factor analysis is a standard statistical technique for identifying the latent variables or factors contributing to variations in a set of measurements or observed variables, based on the correlations among the observed variables. For example, an individual who reports a higher than average proportion of red at a particular chromaticity is more likely to report more red in nearby chromaticities. Thus, the measurements for these stimuli will covary, presumably because they both depend on the influence of a common process. Factor analytic techniques have been widely used to explore properties of the visual system [e.g. de-Wit and Wagemans (2016), Jones (1948), Peterzell (2016), Thurstone (1944), Wilmer (2008)], and in particular, to examine the mechanisms of color vision and chromatic processing (Burt, 1946; Dobkins, Gunther, & Peterzell, 2000; Gunther & Dobkins, 2003; Peterzell, Chang, & Teller, 2000; Peterzell & Teller, 2000; Pickford, 1946; Webster & MacLeod, 1988). In some cases this approach can provide precise quantitative information about the mechanisms and how they vary across individuals. For example, individual differences in color matching result from several well-characterized processes that influence spectral sensitivity, including the densities of inert screening pigments and the absorption spectra of the photopigments, and factor analysis can be used to identify and parcel out these different sources of sensitivity variation and specify their relative contributions to color matching as well as their values for individual observers (MacLeod & Webster, 1988; Webster & MacLeod, 1988). In many other cases we know much less about the processes limiting perception and performance. However, factor analysis can still provide a valuable tool for constraining the possible models of these processes.

Here we used factor analysis to explore the basis for interobserver variations in hue scaling. We reasoned that if these scaling functions did reflect the activity of two processes signaling red-green and blue-yellow sensations, then these processes should be evident in the patterns of variation revealed by the factor analysis. That is, the analysis should reveal a small set of general factors corresponding to the opponent primaries. To test this, we analyzed two datasets, one from a previous study that measured hue-scaling functions for 59 observers (Malikoc, Kay, & Webster, 2005), and a second that was collected for the present study. The latter was added to provide a finer sampling of both the stimulus set and the scaled responses, and because we were also interested in relating the percepts of the observers (as measured by the scaling) to measurements of how they verbally labeled the hues. We report the relationship between hue scaling and color naming in the accompanying paper (Emery, Volbrecht, Peterzell, & Webster, 2017). Here we focus on the hue-scaling functions and how they differ across observers, and what those differences imply about the visual representation of color.

2. Materials and methods

2.1. Participants

The participants included 26 graduate and undergraduate students from the University of Nevada, Reno ranging from ages 18 to 47. A 27th observer was excluded based on the high variability of their settings. Sixteen of the observers were female. Undergraduate students were provided extra credit in exchange for their participation. All observers had normal color vision as assessed by the Cambridge Colour Test, as well as a contrast threshold task, and all had normal or corrected-to-normal visual acuity. Each observer participated with informed consent, and all procedures followed protocols approved by the University of Nevada, Reno’s Institutional Review Board, and were conducted in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2. Stimuli

Stimuli were presented on a SONY Multiscan 500PS Trinitron CRT monitor controlled with a Cambridge Research Systems ViSaGe Stimulus Generator, providing 12-bit resolution per gun. The monitor was calibrated with a Photo Research PR 655 spectroradiometer with gun outputs linearized with a gamma correction. The stimuli had a constant luminance of 20 cd/m² and were shown on an 11.3 by 8.5 gray background that had the same luminance as the test stimuli, and the chromaticity of Illuminant C (CIE 1931 x, y = 0.31, 0.31). Luminance was based on photometric measurements and thus stimuli were not adjusted to be equiluminant for individual observers. The test chromaticities were based on a variant of the MacLeod-Boynton (MacLeod & Boynton, 1979) chromaticity diagram, scaled based on previous studies (Webster,
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