Environmental Influences on Color Vision

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Definition

It is evident that color vision evolved to inform organisms about their environment and thus must be shaped by the environment the organism is in. The color properties of the world are a potent factor affecting not only the basic mechanisms of color vision within a species but also how they are calibrated and fine-tuned within the individual. As a result, many aspects of the physiology of color coding and the phenomenology of color experience can be predicted by looking outside the observer – to analyze the signals available in the color environment. The following provides a number of specific examples of how knowledge of the color characteristics of the environment has helped to account for some of the known properties of our color vision.

Environmental Signals and the Evolution of Color Vision

A central principle in understanding the design of sensory systems has been coding efficiency – or how to transmit the most information about the stimulus using the least resources. The assumption that vision maximizes coding efficiency provides a powerful link between the properties of the stimulus and the properties of the observer [1] and has led to a surprising number of insights about the early stages of color vision and how they are optimized for the color characteristics of the environment. For example, natural color spectra (of both illuminants and surfaces) typically vary gradually with wavelength and thus can be captured with a small number of spectral samples [2]. This may in part be why color vision is typically low dimensional (e.g., based on three classes of photoreceptors in trichromatic observers). The fact that spectra can be represented by a small number of dimensions has also been a central insight into understanding the capacity and limits of color constancy (e.g., the ability to perceive that the color of a surface has not changed even when the light falling on it has).

Scenes are composed of collections of many spectra, and these color distributions have characteristic properties. For example, most luminances and chromaticities tend to be near the average, or gray. This property has been used to predict how neurons respond to different intensity or color levels in the image. To code these efficiently, responses should change most rapidly near gray, where signals are more frequent and thus require better discrimination, and asymptote at the extremes (e.g., highly saturated colors), where signals are rare. Thus the color statistics of images can directly account for the sigmoidal response functions of visual neurons and for the fact that we are best at discriminating small color differences near gray [3].

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Color vision requires comparing the differences between the responses of receptors with different spectral sensitivities. Because the sensitivities are broad and overlapping, and because as noted spectra vary gradually, the signals within the different cone classes are highly correlated. This redundancy can be removed by recoding the cone signals into "luminance" mechanisms (e.g., in cells that receive excitatory inputs from different cones and thus sum their inputs to represent luminance) and "chromatic" mechanisms (e.g., in cells that instead receive excitatory inputs from one cone type and inhibition from another, so that the response depends on the difference or ratio of the cones' signals). Thus redundancy reduction provides a rationale for how the cone signals are reorganized in cells in the retina [4]. Finally, the overlap in the cone sensitivities also means that the differences between the cones (which convey color) are many times smaller than the absolute responses (which convey luminance). If our vision depended on these raw cone signals, then the world would vary much more in brightness than in color. However, a further prediction from coding efficiency is that each channel uses its fully dynamic range to code the range of available signals. As a consequence we are much more sensitive to chromatic differences than luminance differences (when equated for cone contrasts), and the range of brightness and color in the world appears perceptually balanced.

The preceding examples illustrate how studies of the color environment have provided insights into general properties of the mechanisms of color vision. For many species the environment also holds special color signals that are important to detect, because they signal food or mates, and these signals have given rise to more specialized adaptations. For example, most mammals are dichromats, yet humans and other old-world primates evolved a third class of photoreceptor through an evolutionarily recent duplication of the gene coding their longer-wave photopigment. The extra dimension of color afforded by their trichromacy has been shown to be well tuned for detecting ripe fruit among foliage and also for judging the subtle variations in skin tones that signal the health and emotional state of conspecifics [5].

Color Appearance and the Color Environment

Conventional models of color appearance hold that the signals from the three classes of cones are recombined to form three perceptual channels that signal red vs. green, blue vs. yellow, and bright vs. dark. A central issue in color science is how these perceptual dimensions are encoded by neurons of the visual pathway and why particular hue directions are special. Here again the color characteristics of the environment are thought to play a central role.

According to the standard color-opponent model, any stimulus is represented by how it differs from gray (e.g., lighter vs. darker or redder vs. greener). But what establishes gray? The spectral sensitivity of the observer varies in capricious ways depending on factors such as the level of screening pigments or the relative numbers of the different types of cone receptors and thus must be adjusted to match "gray" in the environment. This gray likely corresponds to the average spectral stimulus the observer has been exposed to. Normalizing color responses for this average probably happens at many levels of the visual pathway and at many timescales. For example, the photoreceptors rapidly adapt to changes in the average color or brightness of the scene (e.g., becoming more or less sensitive when the light levels get lower or higher, respectively). These sensitivity changes rescale their relative responses so that the current average color tends toward gray, an adjustment known as von Kries adaptation, and this is thought to be an important initial component in color constancy (since it tends to remove or discount changes in the average color of the scene introduced by changes in the illuminant). Similarly, opponent channels must be calibrated so that the opposing cone inputs are weighted so that their null points (e.g., where the signal is neither red nor green) correspond to a neutral gray. Sensory adaptation thus plays a critical role in calibrating color vision so that it is correctly adjusted to match the observer's environment [6]. (Importantly, these adaptive responses are not unique to color, but probably influence all aspects of perception.)

Supporting this, many lines of evidence show that the stimulus that appears gray depends very little on the observer's actual sensitivity to wavelength. For example, individuals vary widely in the density of the lens pigment, which also steadily builds up with age. This pigment selectively absorbs at shorter wavelengths, and thus the light reaching the retina of an older observer will have a very different spectrum from a typical young observer. Despite this, the physical stimulus that appears white remains constant across the lifespan, because color mechanisms are continuously recalibrated so that they are adjusted to the average spectrum [7]. Receptors in the fovea at the center of vision are also selectively screened by a second inert pigment known as macular pigment, which further filters light at short wavelengths. Thus the fovea and surrounding periphery receive very different stimulation on average. Yet the physical stimulus that looks white again remains largely constant across the visual field, suggesting that each part of the eye can locally adapt to set the achromatic point. Patients undergoing cataract surgery provide a natural experiment for observing these adaptation processes. Cataracts represent an extreme form of lens brunescence, blocking much of the short-wavelength light. Yet the stimulus that appears white is within the normal range for many patients. When the cataract is replaced with a clear lens, the sudden increase in short wavelengths causes the world to appear too blue. However, achromatic settings almost immediately begin to renormalize and continue to slowly drift back to their prior levels over a period that may last for months [8].

Analogous arguments have been advanced to account for the special nature of red-green and blue-yellow as the primary dimensions of color appearance. As noted above, red may be special because it signals ripe fruit or blood. For blue and yellow, a number of studies have pointed out that these hues fall close to the daylight locus (e.g., variations between the sky and direct sunlight), and thus the tuning of the blue-yellow axis is matched to a dominant source of variation in the color environment [9]. In fact, this idea has been taken further to suggest that the special perceptual nature of some hues lies entirely in the environment. In opponent theory, blue and yellow (and red and green) are pure or unique hues because they arise from the pure isolated responses within the blue-yellow or red-green channels. However, a problem for this theory is that neurons with the chromatic tuning predicted by these sensations (e.g., that respond only to pure blue-yellow signals) have yet to be discovered. This has suggested the possibility that observers may learn to perceive the unique hues as special because they are special in the environment and not because they correspond to a unique pattern of activity within the neurons coding color. The number of basic color terms (color words that have high agreement and do not refer to specific objects) and the locations in color space that they denote have also been predicted from analyses of how colors are clustered in images. By this account, red spectra tend to form a distinct and distant cluster of signals, and this salient cluster may be why a prevalent color term for red arose in many of the world's languages [10].

Regardless of their neural basis, it is clear that like gray, the unique hues are not strongly tied to the specific spectral sensitivity of the observer. The wavelength that appears pure yellow shows little dependence on the relative numbers of long- and medium-wavelength-sensitive cones, even though these can vary over an enormous range of ratios. Similarly, the wavelengths chosen as unique hues cannot be predicted from individual differences in lens or macular pigment density and like gray show little effect of the observer's age. These results could again suggest that the hues are set more by the environment. However, it is important to note that the stimuli perceived as unique hues also vary widely across observers and thus cannot be tightly bound to pronounced and stable properties of the world. Indeed, it remains debated to what extent and in what ways color appearance and color naming reflect properties of the observer, the physical environment, or the cultural environment [11].

A further potential tie of the appearance of blue and yellow to the environment is that, in a number of tasks, observers appear less sensitive to this color axis. For example, when individuals adjust a stimulus to appear white, they are much more tolerant of blue-yellow variations than red-green variations, and differences in the achromatic settings between observers also exhibit greater variance in blue and yellow. Similarly, color discrimination thresholds are (in some but not all cases) higher for blue and yellow. At
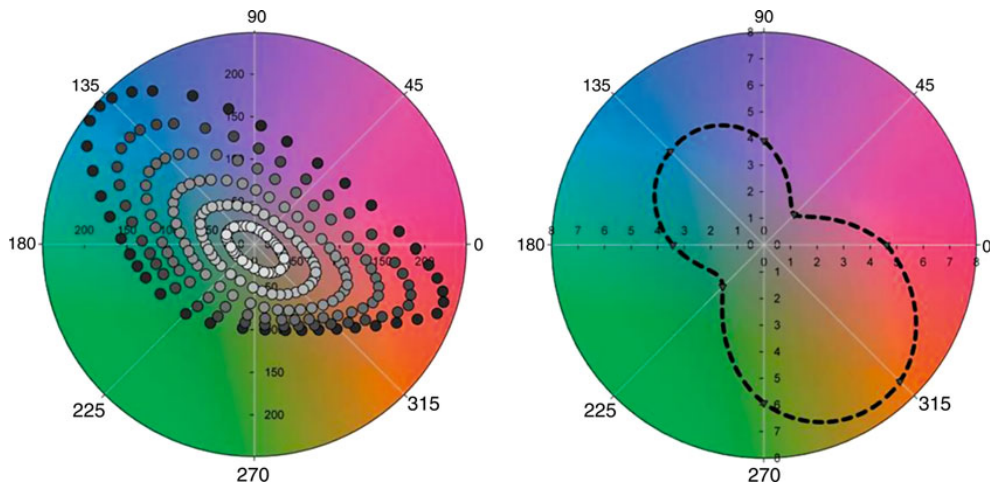
Fig. 1 Uniform color systems and natural image statistics. *Left*: Munsell colors plotted within a color space defined by the two color-opponent axes coded by the retinal: long- versus medium-wavelength cone signals (x axis) and short versus medium and long cone signals (t axis). Sets of points with the same shading represent contours of constant chroma. These are elongated in the bluish-yellowish direction, consistent with weaker sensitivity to these hue directions. *Right*: color distribution characteristic of natural outdoor scenes plotted in the same space. The scenes have a blue-yellow bias corresponding to the sky and earth. Note that the scaling is chosen to equate sensitivity to each axis, and this roughly matches the range of color along either axis. The weaker sensitivity to blue and yellow may be an adaptation to the greater blue-yellow variance in environmental color

suprathreshold, blue-yellow variations can have lower effective contrast (e.g., in a color search task), are rated as lower in visual discomfort (which correlates with perceived contrast), and have recently been found to induce weaker cortical responses as measured by functional MRI. One potential explanation for this bias against blue-yellow is that the world itself has a bias toward more blue and yellow. In particular, in many natural outdoor scenes, the variance in chromaticity is higher along bluish-yellowish axes [12]. The visual system adapts not only to the average color in the stimulus but also to the range or contrast. Adaptation to the higher blue-yellow contrasts in typical outdoor scenes may thus leave us less sensitive to these hues. Notably, this bias is also built into the structure of perceptually uniform color spaces (Fig. 1). Color order systems like the Munsell system or spaces like the CIE uniform chromaticity diagram are also stretched along bluish-yellowish axes (though these tend to be closer to an orange-cyan axis). Not surprisingly then, uniform spaces may mirror the structure of the color distributions we are adapted to and in turn might hold clues to the particular color environment we are calibrated for [13].

Variations in the Color Environment

Clearly, the world is not stationary in its color characteristics and can instead vary widely from one location to the next or in the same place over time as the lighting or seasons change [12]. If observers are adapted to the colors they are immersed in, then we should expect variations in the properties of their color vision as we go from forest to desert or from summer to winter (Fig. 2). The effects of such environmental changes have not been widely studied, but there are telling signs that they occur. One example is variations in visual sensitivity that could arise from different levels of exposure to the phototoxic effects of sunlight. Exposure to ultraviolet light accelerates the normal yellowing of the lens with age and thus reduces sensitivity to blue. Brown and Lindsey noted an intriguing correlation between areas of the world with high UV-B (at lower latitudes) and the presence of languages which lacked a distinct basic color term
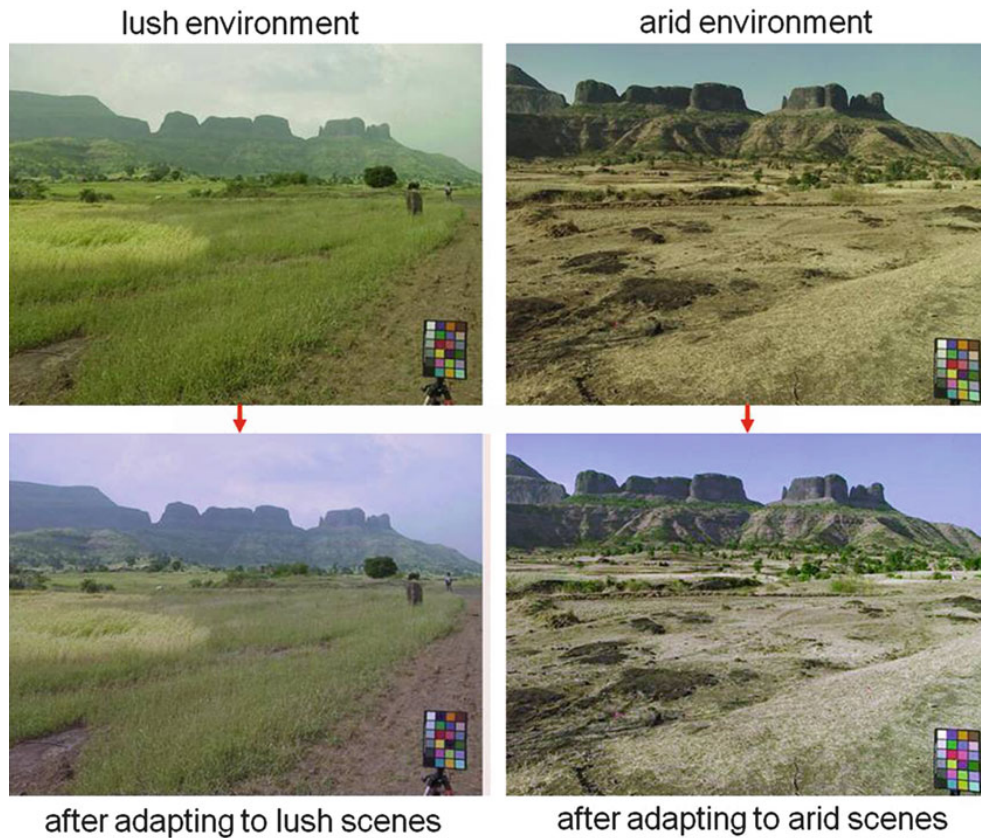
Fig. 2 Simulations of how the world might appear to observers adapted to different environments. *Top*: images of the same setting in wet (*left*) or dry (*right*) seasons. *Bottom*: the same images with the colors adjusted to simulate the effects of visual adaptation to the average color and to the range of colors in the different settings. Note this shifts the average color toward gray and tends to highlight the more novel colors in the environment (Reproduced with permission from Juricevic. I. and Webster, M.A. (2009). Variations in normal color vision. V. Simulations of adaptation to natural color environments. Visual Neuroscience 26, 133–145)

for blue [14]. They suggested that populations in high UV-B areas would have more deficient sensitivity at short wavelengths and would thus be less likely to experience "blue." On the other hand, as noted above, measures of color appearance do not vary with normal aging of the lens, and thus adaptation may similarly compensate color appearance for these sensitivity losses.

A second example is when observers are placed in artificially colored environments. Neitz et al. exposed subjects for several hours at a time to "red" or "green" worlds by altering their room lighting or by having the subjects wear tinted contacts [15]. This led to persistent changes in the wavelength that appeared unique yellow, consistent with a long-term renormalization in color vision. Subtle differences in color appearance have also been found in studies comparing unique hues and focal colors (the best example of a given color term) across different populations [11]. However, a clear causal link between how much the world varies in color, and how much people in different parts of the world differ in their color perception, has yet to be established.

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