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Notes:

Spectral statistics in natural scenes predict hue, saturation, and brightness

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The perceptual color qualities of hue, saturation, and brightness do not correspond in any simple way to the physical characteristics of retinal stimuli, a fact that poses a major obstacle for any explanation of color vision. Here we test the hypothesis that these basic color attributes are determined by the statistical covariations in the spectral stimuli that humans have always experienced in typical visual environments. Using a database of 1,600 natural images, we analyzed the joint probability distributions of the physical variables most relevant to each of these perceptual qualities. The cumulative density functions derived from these distributions predict the major colorimetric functions that have been reported in psychophysical experiments over the last century.

color | colorimetry | perception | psychophysics | vision

Color percepts are described in terms of hue (the sensation of the relative redness, greenness, blueness, or yellowness of a spectral stimulus), saturation (the degree to which a color percept deviates from neutral gray), and brightness (the apparent intensity of the stimulus). Although color percepts are obviously initiated by the spectral characteristics of light stimuli, a major difficulty rationalizing these color qualities in either neurobiological or psychological terms is that they are not linked in any straightforward way to the physical attributes of the corresponding retinal stimuli (i.e., to the energy distribution in the stimuli, to their relative uniformity, or to their overall power, respectively). Thus varying the physical parameter underlying any one of these perceptual categories changes the appearance of all three qualities in highly nonlinear and interdependent ways (1–8).

These classical psychophysical functions, which are illustrated in the Figs. 1a–6a, can be divided into those measured by color discrimination testing and those revealed in color-matching paradigms. In color discrimination tests, the ability to distinguish equally noticeable (or just noticeable) differences in hue or saturation varies systematically as a function of the wavelength of a monochromatic stimulus (1, 2). In color-matching tests, (i) saturation varies as a function of luminance [the Hunt effect (3)]; (ii) hue varies as a function of stimulus changes that affect saturation [the Abney effect (4, 5)]; (iii) hue varies as a function of luminance [the Bezold–Brücke effect (6, 7)]; and (iv) brightness varies as a function of stimulus changes that affect both hue and saturation [the Helmholtz–Kohlrausch effect (8)]. Explanations proposed in the past have been based on assumptions about neuronal interactions early in the visual pathway and have not led to any consensus (3, 6, 8–11).

Motivated by evidence that natural image statistics predict the response properties of some visual neurons (12) and that image-source statistics predict several aspects of visual perception (13–16), we here examine the hypothesis that this perplexing phenomenology arises from a scheme of visual processing based on statistical covariations of the physical characteristics of light stimuli in typical visual environments. To test this possibility, we acquired a database of 1,600 color images of natural scenes to approximate the range of light stimuli that humans have normally witnessed (see Fig. 7, which is published as supporting information on the PNAS web site). The joint probability distributions of the physical correlates most closely associated with hue, saturation, and brightness were then analyzed

and the cumulative density functions of one attribute given the others determined. We show that the major colorimetric functions are surprisingly well predicted in this way, supporting the conclusion that color percepts are generated by a fundamentally probabilistic strategy of vision.

Results

Hue Discrimination. The human ability to discriminate small changes in hue, measured by just noticeable (or equally noticeable) differences, varies systematically as a function of the wavelength of a monochromatic stimulus. This variation defines a remarkably complex function (1): at the same luminance level, the amount of wavelength change needed to elicit reports of just noticeable differences in hue has two local maxima at ≈ 460 and 530 nm and three local minima at ≈ 440 , 480 , and 575 nm, with sharp increases at both ends of the visible spectrum (Fig. 1a).

The explanation of the hue discrimination curve in Fig. 1a in terms of statistical covariations in the light from natural scenes is illustrated in Fig. 1b–d. Fig. 1b shows the joint probability distribution of the physical correlates of hue and brightness, i.e., $P(Hp, Bp)$, which determines the conditional probability distribution of the physical correlate of hue at any given physical correlate of brightness (as illustrated by the dashed line in Fig. 1b), i.e., $P(Hp|Bp)$. The corresponding cumulative density functions were computed by normalizing and accumulating the probability values of $P(Hp|Bp)$ within a local window centered at the physical correlate of hue in question (the black vertical lines in Fig. 1b; see *Methods*). Fig. 1c shows examples of two such functions, corresponding to two different values of the physical correlates of hue (indicated by Hp_1 and Hp_2 in Fig. 1b) at the same value of the physical correlate of brightness (indicated by the dashed line in Fig. 1b). As described earlier, these cumulative density functions should predict the hue seen by observers.

Note that the functions in Fig. 1c have different slopes at p_1 and p_2 . Thus to maintain the same difference in apparent hue (indicated by d), the changes in the corresponding physical correlates, i.e., Δh_1 and Δh_2 , must be different for different values of the physical correlate of hue (Hp). By assessing these differences for many different values of the physical correlates of hue, we determined the changes that would be expected to generate a constant difference in perceived hue over the full visible spectrum. To compare the function generated on this basis with the function obtained in psychophysical studies of hue discrimination, the values of the physical correlates of hue were converted to wavelengths (Fig. 1d; see *Methods*). Comparison of Fig. 1a and d shows good agreement between the complex psychophysical function and the predicted function based on covariations of the physical attributes of light in natural scenes.

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Abbreviations: RGB, red, green, and blue; CIE, International Commission on Illumination.

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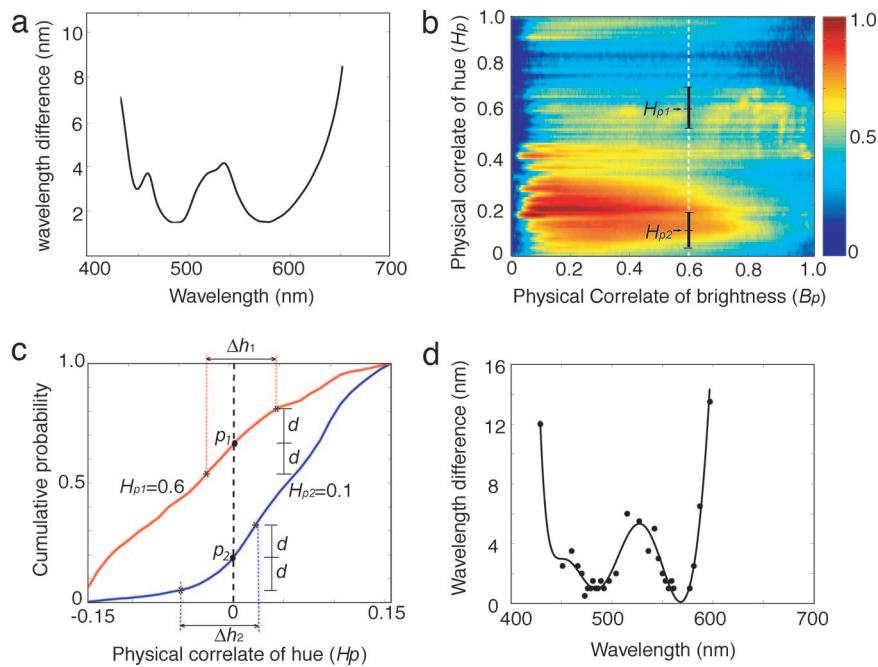


Fig. 1. Statistical explanation of the hue discrimination function. (a) The wavelength change in a monochromatic stimulus needed to elicit a just noticeable difference in hue (after ref. 1). (b) Joint probability distribution of the physical correlates of hue and brightness, $P(H_p, B_p)$, obtained from the image database (probability values in this and subsequent figures are indicated by color coding; see bar on right). (c) Cumulative density functions of $P(H_p|B_p)$ at two different values of the physical correlate of hue ($H_{p1} = 0.6$, $H_{p2} = 0.1$) for the same physical correlate of brightness ($B_p = 0.6$), obtained by normalizing and accumulating the probability values of $P(H_p|B_p)$ within a local window. The abscissa shows the relative value of the physical correlate of hue with respect to the center of the local window. (d) The predicted changes in wavelength needed to maintain constant perceived differences in hue. The points are the constant differences in cumulative density functions at the indicated wavelengths, using 0.02 as a value for d (the scale of d in c has been enlarged for clarity); the solid curve is a polynomial fit.

Saturation Discrimination. The ability to discriminate small changes in saturation measured by the amount of monochromatic light added to white light needed to elicit just noticeable (or equally noticeable) differences in saturation also varies with wavelength (Fig. 2a). At the same luminance level, the psychophysical function defined in this way has a maximum at ≈ 570 nm with decreasing values at both ends of the spectrum (2).

The statistical explanation of the saturation discrimination function is illustrated in Fig. 2b–d. The joint probability distribution of the physical correlates of hue and saturation in the database of natural scenes, i.e., $P(H_p, S_p)$, is shown in Fig. 2b, with examples of the cumulative density functions of $P(S_p|H_p)$ given two different values of the physical correlate of hue (H_{p1} and H_{p2} in Fig. 2b) in Fig. 2c. Points on these functions that have the same cumulative probability values (e.g., p_1 and p_2 in Fig. 2c) should elicit the same perceptual saturation difference with respect to a neutral reference

light, even though they correspond to different values of the physical correlates of saturation (indicated by the dotted vertical lines in Fig. 2c). Given many such values, we could again derive the changes in the physical correlates of saturation needed to maintain the same perceived saturation difference as a function of the physical correlate of hue. To compare these changes with the psychophysical function in Fig. 2a, we converted the values of the physical correlates of hue to wavelengths (Fig. 2d). The predicted changes in the physical correlates of saturation needed to generate the same perceived saturation difference reach a maximum at ≈ 570 nm with decreasing values at the ends of the spectrum, in agreement with the psychophysical observations.

The Hunt Effect. The Hunt effect refers to the observation that the saturation of a stimulus increases as luminance increases, as illustrated in Fig. 3a (3). Fig. 3b shows the joint probability distributions

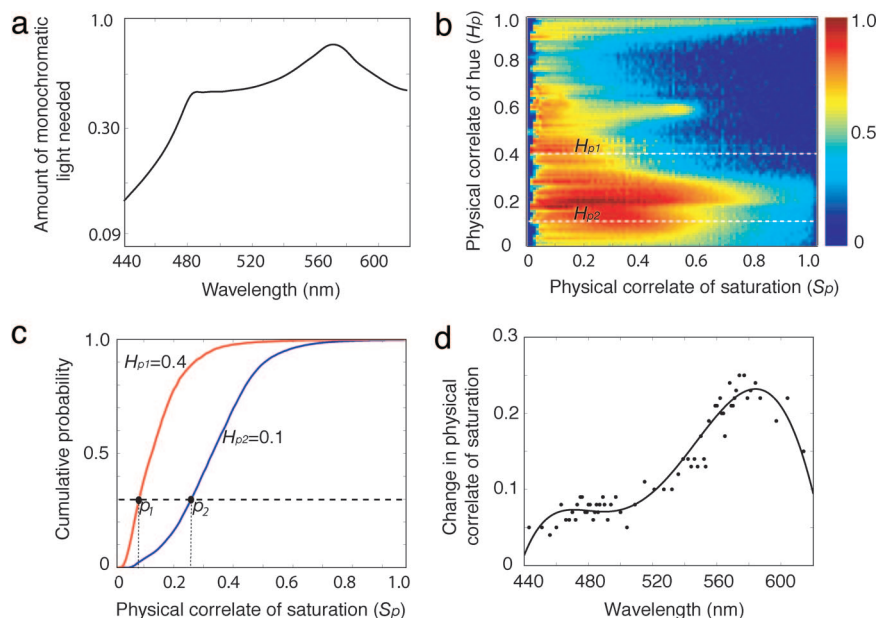


Fig. 2. Statistical explanation of the saturation discrimination function. (a) The amount of monochromatic light needed to generate the same perceived saturation difference with respect to neutral gray at different wavelengths (after ref. 2). (b) Joint probability distribution of the physical correlates of hue and saturation, $P(H_p|S_p)$, obtained from the image database. (c) The cumulative density functions of $P(S_p|H_p)$ when the physical correlate of hue was 0.1 (blue curve; ≈ 575 nm) or 0.4 (red curve; ≈ 515 nm). (d) The predicted changes in the physical correlates of saturation needed to maintain a constant difference in perceived saturation as a function of the wavelength (the value illustrated is 0.3 in the cumulative density function, as shown in c). The points were derived from the cumulative density functions at the indicated wavelengths; the solid curve is a polynomial fit.

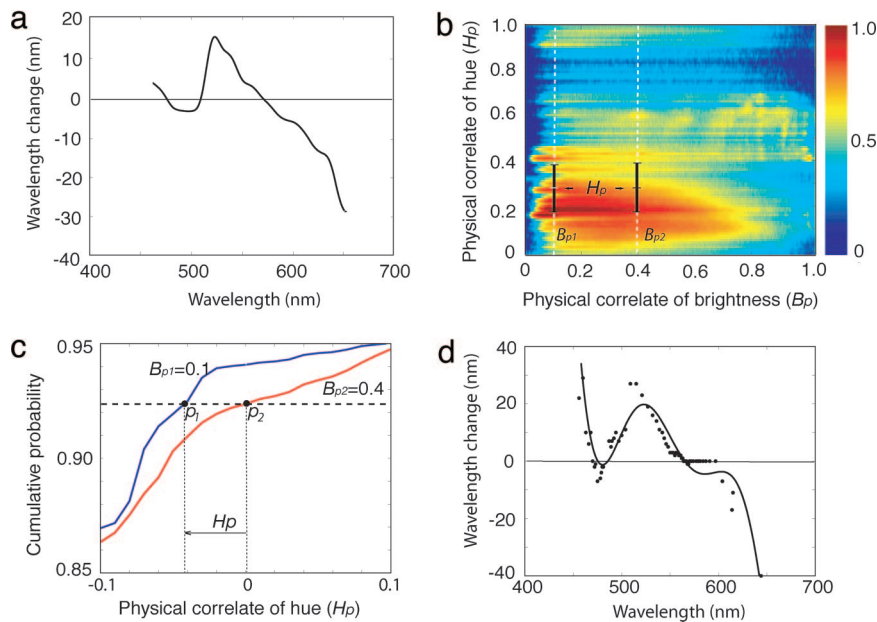


Fig. 5. Statistical explanation of the Bezold–Brücke effect. (a) Psychophysical data showing the changes in wavelength needed to match the hue of a monochromatic light presented at a higher intensity (after ref. 6). (b) Joint probability distribution of the physical correlates of hue and brightness, $P(H_p, B_p)$, obtained from the database. (c) The cumulative density functions of $P(H_p|B_p)$ calculated within a ± 0.1 window centered at 0.3 as the value of the physical correlate of hue, given a lower and a higher levels of the physical correlate of brightness (indicated by the dashed lines in b). (d) The predicted hue shifts for the indicated points; the solid line is a polynomial fit.

$P(H_p, S_p)$. The corresponding cumulative density functions were determined by normalizing and accumulating the probability values of the conditional probability distribution $P(H_p|S_p)$ within a window centered at the physical correlate of the hue in question (indicated by the black bars in Fig. 4b). Fig. 4c shows examples of two such functions (for the values of the physical correlate of saturation indicated by the dashed lines in Fig. 4b).

If points with the same value in the cumulative density functions (e.g., p_1 and p_2 in Fig. 4c) elicit the same apparent hue, then the values of the physical correlates of hue needed to maintain the same perceived hue given different values of the physical correlates of saturation can be derived. The series of pair-wise values [i.e., $(H_{p1}, S_{p1}), (H_{p2}, S_{p2}), \dots, (H_{pn}, S_{pn})$] determined in this way were then converted into corresponding xy values in the CIE chromaticity diagram by using the standard transform (17). The results obtained by repeating this process for many different values of the physical correlates of hue (Fig. 4d) show distortions of the constant hue curves similar to those that define the Abney effect (Fig. 4a).

The Bezold–Brücke Effect. The Bezold–Brücke effect refers to the change in apparent hue as a function of luminance, measured by the wavelength change needed to match the perceived hue of a monochromatic light at a higher luminance level with another monochromatic stimulus at a lower luminance level (6, 7). As shown in Fig. 5a, some monochromatic wavelengths (the locations where the curve intersects the 0 line) are relatively resistant to changes in hue at different intensities, creating a complex psychophysical function that divides the spectrum into regions characterized by oppositely directed hue shifts.

Fig. 5b shows the joint probability distributions of the physical correlates of hue and brightness, i.e., $P(H_p, B_p)$ and Fig. 5c, the corresponding cumulative density functions of the conditional probability distribution $P(H_p|B_p)$ at a higher and a lower value of luminance (dashed lines in Fig. 5b). In the present framework, points on the two functions in Fig. 5c that have the same cumulative probability value (e.g., p_1 and p_2) should elicit the same hue. Thus matching the hue of p_2 under a higher luminance entails point p_1 , which has the same cumulative probability value as p_2 . The difference ΔH_p between the physical correlates of hue at p_1 and p_2 is thus the shift needed for the perceived hue under the lower physical correlate of brightness to match the hue under the higher physical correlate of brightness. By repeating this analysis for a full range of

different physical correlates of hue, we determined the curve that describes the shift of the physical correlates of hue at lower luminance as a function of the physical correlates of hue at a higher luminance. The function in Fig. 5d was generated by converting the physical correlates of hue into wavelengths. Comparison of Fig. 5a and d shows good general agreement with the psychophysical data.

The Helmholtz–Kohlrausch Effect. Finally, the Helmholtz–Kohlrausch effect refers to the observation that at constant luminance, the brightness of a stimulus changes as a function of the physical correlates of both saturation and hue (8). The effect is typically illustrated in terms of isobrightness contours in a CIE chromaticity diagram, as in Fig. 6a. Thus, if the physical correlate of hue is held constant, brightness of a stimulus increases with the physical correlate of saturation; conversely, if the physical correlate of saturation is held constant, brightness changes systematically as a function of the physical correlate of hue.

Fig. 6b shows an example of the joint probability distribution of the physical correlates of saturation and brightness [i.e., $P(S_p, B_p)$] at a constant value of the physical correlate of hue. Fig. 6c shows the cumulative density functions of $P(B_p|S_p)$ at two physical correlations of hue and saturation. Given a constant level luminance (the dashed line in Fig. 6c), we determined the values of the physical correlates of saturation needed to maintain the same cumulative probability value given different values of the physical correlates of hue. In this way, we obtained paired values of the physical correlates of hue and saturation [i.e., $(H_{p1}, S_{p1}), (H_{p2}, S_{p2}), \dots, (H_{pn}, S_{pn})$]. By converting these data into corresponding xy coordinates in the CIE chromaticity diagram (17), we could plot the predicted isobrightness curves (Fig. 6d). Comparison of Fig. 6a and d shows that the functions predicted from the analysis of natural scenes generally accord with the isobrightness functions that define the Helmholtz–Kohlrausch effect.

Discussion

We have examined the idea that the perceptual qualities of hue, saturation and brightness are determined by statistical covariations in the physical characteristics of light in nature, the biological rationale being a means of relating inevitably ambiguous spectral information in retinal stimuli to the real-world sources that observers must respond to (14). In this framework, the cumulative density functions derived from the conditional probability distributions of

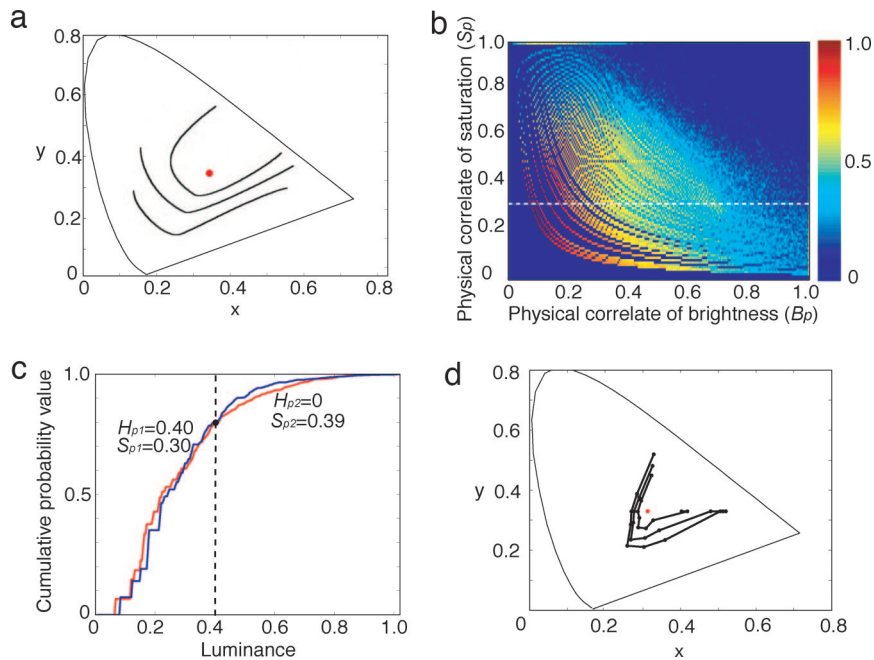


Fig. 6. Statistical explanation of the Helmholtz-Kohlrausch effect. (a) Psychophysical changes in brightness as a function of both hue and saturation, plotted in the 1931 CIE chromaticity diagram (after ref. 8; the red dot indicates the white point). (b) Joint probability distribution of the physical correlates of saturation and brightness, $P(S_p, B_p)$, at a particular value of the physical correlate of hue ($H_p = 0.1$). (c) The cumulative density functions of the physical correlate of brightness when the physical correlate of saturation is 0.3 and the physical correlate of hue 0.4 (blue curve) and when the physical correlate of saturation is 0.39 and the physical correlate of hue 0 (red curve). The cumulative probability values in these functions at a physical correlate of brightness value of 0.4 are the same. (d) The equal-brightness curves predicted by these statistics. Each of the points on a given curve has the same physical correlate of brightness value (0.2) and the same predicted brightness. The relative closeness of these curves reflects the limited number of highly saturated samples in the database and the limited gamut of the xy values in the CIE chromaticity diagram that can be represented by RGB values.

the physical attributes underlying each of these sensations should predict the hue, saturation, and brightness elicited by spectral stimuli in classical colorimetry.

Analysis of the image database shows that, as might be expected, the physical attributes of light from natural scenes (i.e., the physical correlates most closely associated with hue, saturation, and brightness, respectively) covary in specific ways (see Figs. 1b–6b). As a result, the probability distributions of one attribute, given values of the other two attributes, vary systematically. The reasons for at least some of these physical covariances are not hard to understand. For example, the peaks in the joint probability distributions of the physical correlates of hue and brightness (Fig. 1b) and of hue and saturation (Fig. 2b) presumably reflect the fact that light from natural scenes is especially rich in middle wavelengths (18). The results we report show that these statistical covariations predict the full range of classical colorimetry functions surprisingly well.

Many other explanations of these phenomena have been proposed over the years. Most investigators have sought to rationalize colorimetric functions as epiphenomena of early visual processing (see refs. 3, 6, 8–11, 19–21; see ref. 22 for a related review). For example, the hue and saturation discrimination functions in Figs. 1a and 2a can be computed by modeling combinations of the outputs of cone classes or color channels (r-g, y-b, luminance) to small variations in wavelength or color purity (9–11, 19–21). Similarly, some studies have successfully rationalized the Hunt, Abney, and Bezold-Brücke effects as nonlinear combination of cone (9) or color channel responses (21). Others have also used statistical estimation theory to derive hue and saturation discrimination functions (23, 24).

From the perspective of the present framework, this variety of earlier results makes good sense. If the visual system generates color percepts reflexively according to the frequency of physical co-occurrences in the relevant stimuli experienced during evolution, the existing physiological apparatus at all levels of the visual system should have evolved to facilitate neuronal responses that reflect the statistical associations needed to contend successfully with the inherent ambiguity of light stimuli. In other words, from this perspective, the cone fundamentals would have evolved to efficiently use the statistical regularities we have described here. For example, Barlow (25) has argued that the differences in spectral responses among cones represent a balance between wavelength

discrimination and acuity. Thus, the 30-nm difference in sensitivity between the L and M cones means that their signals will be highly correlated, leading to higher achromatic contrast and better acuity. Conversely, S cones are sparse, so as not to affect contrast and 100 nm removed in sensitivity to enhance wavelength discrimination and to cover the rest of the spectrum. The present observations suggest that this arrangement evolved to take advantage of the statistical characteristics in natural spectral stimuli. Our results are similarly consistent with the idea that the color opponent channels evolved to contend with the statistical regularities of the natural visual stimuli. Although the classic perceptions of hue, saturation, and brightness were tested by using visual stimuli generated in laboratory and rarely found in nature, the way the subjects perceive the stimuli, according to our hypothesis, would have been shaped by natural scene statistics. The generally good agreement between our predictions of the full range of colorimetry functions based on light in natural images and the psychophysical data supports this interpretation. Other evidence has already shown that the responses of visual neurons reflect the statistical characteristics of natural visual stimuli (23, 26–31). These neurophysiological findings accord with the implication that the complex interdependence of hue, saturation, and brightness described in colorimetric experiments is the result of a visual processing scheme determined by statistical covariations of the physical attributes underlying these perceptual qualities.

In sum, the success of this statistical framework in explaining these otherwise puzzling colorimetry functions [and at least some of the effects of spatial context on color (15)] implies that the color percepts elicited by any light stimulus are determined statistically according to past human experience, rather than by the features of the stimulus as such. If this idea is correct, then the behavior of color-sensitive neurons at all levels of the primary visual pathway will eventually need to be understood in these terms.

Methods

Conceptual Framework. The fact that retinal images cannot uniquely specify their physical sources has led a number of vision scientists to consider the possibility that visual percepts might be generated statistically (12–16). Let $P(x)$ be the probability distribution of a physical variable x and $P(y)$ the distribution of the corresponding variable y in perceptual “space.” In terms of probability theory,

$P(x)dx = P(y)dy$. To use the full perceptual range, the probability distribution must have maximum entropy and thus be approximately flat (see Fig. 8, which is published as supporting information on the PNAS web site). $P(y)$ is therefore constant, $dy \sim P(x)dx$ and $y(x) \sim \int_{x_{\min}}^x P(x')dx'$, which is the cumulative density function of x . Because the value of a physical variable x underlying any point in a natural stimulus (e.g., its luminance) is correlated with other physical variables (e.g., the distribution of spectral power and its relative uniformity), the perceptual variable y will be determined by the conditional cumulative density function of x . Cumulative density functions derived from natural scenes have already been used to model neuronal responses to contrast (26), to evaluate optimal nonlinear coding (31), and to rationalize brightness contrast effects (16).

In this conception, any psychophysical function that entails hue, saturation, and brightness should be predicted by the conditional cumulative density function of the physical variable underlying the quality tested (these variables are further discussed in *Supporting Text*, which is published as supporting information on the PNAS web site). Accordingly, the same value in any two cumulative density functions should elicit the same percept, and a given difference in such functions should elicit the same perceptual difference.

Acquisition and Calibration of the Natural Image Database. To examine whether this framework can indeed rationalize colorimetric psychophysics, we acquired a database of 1,600 images of natural scenes to serve as a proxy for human color experience (see Fig. 7). Although the database would ideally comprise hyperspectral images, this is not practical at present. We therefore used a digital camera (Olympus C2040, Melville, NY) to take high-quality color red, green, and blue (RGB) images of fully natural visual environments. The images were obtained at different locations in the southern U.S. in all four seasons during the hours of full daylight and included a variety of natural terrains with objects at distances of <1 m to thousands of meters. The purpose of image calibration is to map the camera RGB values to a standard linearized RGB space. Thus we first determined the response functions of the camera RGB channels by measuring 70 pair-wise measurements of raw and linearly transformed RGB values for each exposure setting. We then used these functions to correct the raw RGB values of each image pixel to linear and standard RGB values (see *Supporting Text* and Fig. 9, which is published as supporting information on the PNAS web site, for further details).

Physical Correlates of Hue, Saturation, and Brightness. To test whether the major colorimetric functions can be explained statistically requires quantitative representation of the physical variables that correlate most closely with the perceptual qualities of hue, saturation, and brightness, respectively. For this purpose, we used the hue, saturation, and value (HSV) color space model (32) (see *Supporting Text*).

Predicting Color Percepts Using Cumulative Density Functions. To predict colorimetric functions, the hue, saturation, and value (HSV) triplet values derived from the corrected RGB values of each image pixel were used to compute the joint probability distributions of the physical attributes of light underlying hue, saturation, and brightness. The basis for the distributions was a compilation of 4.5×10^8 pixels sampled at random from the 1,600 images in the database. We counted and then normalized the frequency of cooccurrence of the physical correlates of brightness (Bp), hue (Hp), or saturation (Sp) to obtain the joint probability distributions of: (i) the physical correlates of hue and saturation, $P(Hp, Sp)$; (ii) the physical correlates of hue and brightness, $P(Hp, Bp)$; and (iii) the physical correlates of saturation and brightness, $P(Sp, Bp)$. From these distributions, we determined directly the one-dimensional conditional probability distribution for each physical attribute, given values for the others. The cumulative density functions used to predict colorimetric functions were then computed from these one-dimensional conditional probability distributions by accumulating the relevant probability values (see *Supporting Text*). Particular values of x in the conditional cumulative density function $F(x|X)$ were determined by the sum of the probability values of all variables x' less than or equal to x , i.e., $F(x|X) = \sum_{x' \leq x} P(x'|X)$, where $x_{\min} < x < x_{\max}$ and x_{\max} and x_{\min} are the maximum and minimum, respectively, of all of the possible values of x , and X is the set of given physical variables correlated with x . Because brightness and saturation are ordinal percepts, the cumulative probability values were computed over the full range of their physical correlates (i.e., $x_{\min} = 0, x_{\max} = 1$). Because sensations of hue are circular, these cumulative probability values were computed over a local range centered at the value of the physical correlate of the hue (Hp) in question (i.e., $x_{\min} = Hp - \Delta w$ and $x_{\max} = Hp + \Delta w$, where Δw is the width of the window). When $Hp - \Delta w$ was < 0 , the determination was begun from 1; and when $Hp + \Delta w$ was > 1 , the determination was begun from 0.

To compare these statistical analyses to the relevant psychophysical functions, we mapped the physical correlates of hue to the corresponding wavelength values used in psychophysical experiments. The mapping was generated by converting each spectrum to corresponding RGB values and then to HSV values, using the standard transformation described earlier (17, 32). Because colorimetry is carried out with monochromators that have some uncertainty arising from backlash, the monochromatic light at each wavelength from 400 to 700 nm was assumed to be a narrow-band Gaussian function.

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