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The color of night: Surface color perception under dim illuminations

JOEL POKORNY,¹ MARGARET LUTZE,¹ DINGCAI CAO,^{1,2} and ANDREW J. ZELE¹

¹Department of Ophthalmology and Visual Science, University of Chicago, Chicago, Illinois ²Department of Health Studies, University of Chicago, Chicago, Illinois

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Abstract

Several studies document rudimentary color vision under dim illumination. Here, hue perceptions of paper color samples were determined for a wide range of light levels, including very low light levels where rods alone mediate vision. The appearances of 24 paper color samples from the OSA Uniform Color Scales were gauged under successively dimmer illuminations from 10-0.0003 Lux. Triads of samples were chosen representing each of eight basic color categories; red, pink, orange, yellow, green, blue, purple, and gray. Samples within each triad varied in lightness. Observers sorted samples into groups that they could categorize with specific color names. Above 0.32 Lux, observers sorted the samples into the originally chosen color groups with few exceptions. For 0.1–0.01 Lux, the red and orange samples were usually correctly identified as either red or orange. The remaining samples tended to be grouped into two categories, associated with the scotopic sample reflectance. The lowest reflectance samples were below threshold and were named black. The higher reflectance group was named predominately as green or blue-green (three observers; the fourth observer used blue or achromatic). At the three dimmest levels (≤ 0.0032 Lux) there continued to be conspicuous color percepts. Color categories were reliably assigned based on relative sample scotopic lightness. Of the samples above threshold, those with lower reflectance were classified as red or orange (all observers) and the higher reflectance samples as green or blue-green (three observers) or achromatic or blue (the fourth observer). Rods and L-cones presumably mediated color percepts at the intermediate light levels used in the study. At the three lowest light levels there were distinct color appearances mediated exclusively by rods. We speculate that at these light levels the visual system estimates probable colors based on prior natural experience.

Keywords: Photopic, Mesopic, Scotopic, Rod color, Color appearance

Introduction

Human vision maintains a perceptual stability through the transition between daylight and twilight conditions in which real world objects, with broad reflectance spectra, do not abruptly change color with diminution in light level. Rather there is a gradual reduction in saturation and color gamut with decreasing light levels. Several studies document rudimentary color vision under dim illumination conditions (Middleton & Mayo, 1952; Schneider & von Campenhausen, 1998; Ishida, 2002; Shin et al., 2004). A challenge has been to devise a set of stimulus and viewing conditions that afford evaluation of the receptor types that mediate the color percepts under dim illuminations.

What are the receptoral mechanisms that are responsible for color perception as illumination is reduced? With daylight illumination, cones dominate vision; the rod system is in saturation for all but the longest wavelengths, and their contribution is minimal (rods in saturation are not capable of signaling stimulus change). With reduction in light level from daylight to twilight, rods begin to play an active role, and both rods and cones contribute to visual perception. Further reductions in light level lead to a selective loss in S-cone sensitivity (Brown, 1951; Verriest et al., 1963; Walkey et al., 2001) and a progressive increase in rod sensitivity. Whereas L- and M-cones remain active, percepts are mediated primarily by the rods and L-cones, because rods are more sensitive to mid- and short-wavelength light. The dominance of the rods and L-cones is related to the Purkinje shift.

Purkinje (1825) described changes in the brightness of different colored objects with variation in light level. As the rods gradually become dominant during dark-adaptation, the peak of visual sensitivity shifts toward shorter wavelengths so that objects predominantly reflecting mid- and short-wavelength light look relatively brighter than objects that reflect long-wavelength light. The Purkinje shift reflects the fact that the cone luminous efficiency function peaks at 555 nm, whereas the rod luminous efficiency function peaks at 507 nm. In terms of relative rod and cone sensitivities, for wavelengths >650 nm, the dark-adapted rod and cone thresholds are about equal (Hecht & Hsia, 1945; Wald,

Address correspondence and reprint requests to: Joel Pokorny, Visual Science Laboratories, University of Chicago, 940 East 57th Street, Chicago, IL 60637. E-mail: j-pokorny@uchicago.edu

1945). Thus for long-wavelength stimuli, with reduction in light level there is no situation where rods alone mediate vision. With progressively shorter wavelengths however, rod sensitivity increases relative to cone sensitivity, being a factor of 1000 or greater in the mid- and short-wavelength regions of the spectrum (Kohlrausch, 1931).

In summary, at high light levels cones predominate and as light levels lower there is a region where both rods and all three cone-types are active. At lower light levels the S-cones go below threshold and the rods begin to dominate in the mid- and shortwavelength regions. Finally, at very dim light levels vision is determined solely by rods. In this study we used a group of simultaneously presented paper color samples. The samples were chosen to be representative members of the eight basic noncontrast color categories defined by Boynton and Olson (1987). We determined hue percepts for a wide range of light levels including very low light levels at which cones do not contribute to color perception.

Materials and methods

Stimuli and apparatus

The stimuli were 24 paper color samples from the Optical Society of America Uniform Color Scales (OSA-UCS), which is an atlas with regular rhombohedral sampling of color space (Kuehni, 2003). The colors chosen for this study were triads of samples representing each of the 8 basic color categories used by observers to describe the non-dark appearing colors (Boynton & Olson, 1987); red, pink, orange, yellow, green, blue, purple, and gray. The samples within each color triad varied in lightness. Table 1 gives sample *L*, *j*, *g* values, their measured CIE $10^{\circ} x$, *y* chromaticities and their relative scotopic and photopic luminances. For the highest level of illumination (46.2 Lux), the sample with the highest photopic luminance was Yellow-1 (12 cd/m²), and the sample with the highest scotopic luminance was Blue-1 (16.6 scotopic cd/m²). The photopic ($L_{i,j}$) and scotopic ($L'_{i,j}$) luminances of the sample *i*, at illumination level *j*, may be calculated using the equations,

$$L_{i,j} = \frac{Ev_j}{46.2 Lux} \times RV(\lambda)_i \times 12,$$

and

$$L'_{i,j} = \frac{Ev_j}{46.2 Lux} \times RV'(\lambda)_i \times 16.6,$$

where Ev_j is the illumination level in photopic Lux, and $RV(\lambda)$ and $RV'(\lambda)$ are the relative photopic and scotopic luminances of sample *i* given in Table 1.

The 50-mm square samples were placed in matt black mounts (3 mm borders) that could be moved around on a 0.34 by 0.60 m matt black surfaced viewing table. Each sample subtended 8° to 10° of visual angle when viewed from 0.30–0.35 m. The light source, a 17-Watt rapid start fluorescent lamp (Philips F17T8/TL950, correlated color temperature, 5000 K; color-rendering index, 98) was mounted 1.6 m above the viewing table. An AC regulator (Electronic Research Associates LC-3210) provided 120 V. Coarse adjustment of light level was accomplished using four baffles, one with a rectangular hole (50×527 mm) and three with 15 equally spaced circular holes (diameters of 15.08, 4.76, and 1.59 mm), providing approximately 1.0 log unit steps in attenuation. The baffles preserved uniform illumination of the viewing

OSA-UCS CIE 1964 10° Color L i g х y $RV(\lambda)$ $RV'(\lambda)$ Red 1 $^{-2}$ 4 -100.5877 0.3486 0.353 0.104 Red 2 2 0.3429 0.235 0.090 -80.5634 Red 3 -5 1 -70.5470 0.3264 0.162 0.072 0 0.192 8 -80.5657 0 4 9 1 Orange 1 0 3974 0.3800 Orange 2 -1 5 -7 0.5352 0.453 0.230 $\begin{array}{r} -2 \\ 3 \\ 0 \\ -2 \\ 4 \\ 4 \\ 3 \\ -3 \\ -6 \\ -7 \\ 1 \end{array}$ 6 Orange 3 -100.6052 0.3603 0.346 0.085 Pink 1 -1-5 0.4057 0.3402 0.960 0.890 0 0.4593 0.3326 0.606 0.437 Pink 2 -80 0.243 Pink 3 0.4887 0.3214 0.407 Yellow 1 8 0 0.4353 0.4408 1.000 0.998 Yellow 2 12 0 0.4790 0.4734 0.893 0.773 Yellow 3 11 0.4893 0.779 0.619 -10.4600 5 0.2942 0.4826 0.210 0.375 Green 1 3 2 1 2 Green 2 0 3396 0 4750 0.070 0.106 Green 3 1 0.3466 0.4267 0.051 0.069 Blue 1 -5 3 0.2571 0.3016 0.689 1.000 -5 Blue 2 3 0.1965 0.2367 0.170 0.266 Blue 3 -3 0.2459 0.2615 0.078 0.105 0.5 1.5 -0.50.3647 0.3665 0.732 0.829 Grey 1 0.5 -0.50.3641 0.3658 0.426 0.482 Grey 2 0 -5 Grey 3 $^{-4}$ 0 0.3516 0.3642 0.219 0.257 -3 0.338 0.395 Purple 1 -10.2874 0.2630 -6 $^{-4}$ $^{-2}$ Purple 2 0.3257 0 2592 0.131 0134 Purple 3 -3 -10.3030 0.2604 0.072 0.077

Table 1. Chromaticities and relative luminances of the selected color samples

Color perception under dim illuminations

table surface; there was less than 10% variation across the surface at all light levels. A high-frequency electronic dimming ballast (Advance IZT-32-SC, operating above 42 kHz) allowed fine adjustment of light level, providing continuous adjustment of illumination level over a 1.5 log unit range. The lowest two light levels were created using the baffle with the 1.59 mm holes and an interposed 1.2 log unit neutral density filter sheet (Lee Filters USA, Burbank CA).

The spectral power distributions for each of the 24 OSA-UCS color samples illuminated by the light source were measured at the maximal realizable light output in the experimental setup (46.2 Lux) using a Photo Research PR-650 spot spectroradiometer. Measurements were made at a distance of 0.5 m with an angle of 45°, in accord with the *ASTM* document E1164-93 for object color evaluation (ASTM, 1994). Spectral measurements were recorded at 4 nm intervals and then interpolated to 1 nm intervals. There were small systematic differences between the published CIE 10° *x*, *y* chromaticities of the OSA-UCS samples (MacAdam, 1978) and those calculated based on our measurements. This discrepancy reflects the difference in color temperature of our light source, 5000 K, and the D65 illuminant used by MacAdam (1978).

Procedure

All samples were simultaneously present on the viewing surface. The appearances of the samples were gauged under successively dimmer illuminations in 0.5 log unit steps over a 4.5 log unit range from 10 to 0.0003 Lux (1.0–3.5 log Lux). Sufficient time for adaptation (\geq 10 min) was allotted following each decrease in illumination. At each light level, the observer was initially presented with a random aggregation of the samples, which he or she then sorted into groups that could be categorized with specific color names. There were no restrictions imposed as to the color names an observer could use. The experiment for all light levels was completed in a \sim 2.5 hr session; each observer participated in three sessions.

We performed two control experiments. In Control Experiment 1, the observer reported the color of each sample when presented one-by-one (in the absence of contextual cues from the other samples) at the lowest illumination level ($-3.5 \log Lux$). Control Experiment 2 was a replication of the main experiment but with the pink, orange, and red samples removed.

Color appearance: model predictions

For each sample, the corresponding L, j, g values were converted into L-, M- and S-cone excitations (Cao et al., 2005a). The cone chromaticities of the color samples (ignoring lightness) are shown in a relative cone Troland space (Fig. 1, upper left panel) that is segmented into eight basic non-contrast color regions derived from the data of Boynton and Olson (1987). This represents photopic trichromatic vision.

With successive reductions in illumination, our expectation was that observers would identify the samples according to the photopically chosen categories until a light level was reached where one, or more of the cone types, was below threshold. As outlined in the Introduction, at light levels where rod sensitivity is much higher than M-cone sensitivity, the L-cones and rods might mediate some form of color perception. With further reduction in light level, only the rods may mediate vision.

We calculated the relative photopic, scotopic luminance, and L-cone excitation based on the sample spectral power distributions, the Smith and Pokorny (1975) cone fundamentals and the CIE V'(λ) relative luminous efficiency function (CIE, 1951). This allowed us to specify the relative ratio of the *L*-cone excitation to scotopic luminance for each color sample (*L*-cone/Rod, Fig. 1, upper right panel) and the relative scotopic luminance (Fig. 1, upper right panel). The *L*-cone/Rod values indicate the relative activation level of the *L*-cones to rods for the samples. This panel represents dichromatic mediation of vision. When the light level is below the *L*-cone threshold, only rods are active. The upper right panel of Fig. 1 shows the relative scotopic luminance of the sample. This panel defines a monochromatic, rod input.

Observers

The authors, all with normal color vision (as assessed with the Neitz OT anomaloscope and the Ishihara pseudoisochromatic plate test), served as observers. The Institutional Research Board at the University of Chicago approved all procedures.

Data analysis

For each of the four observers, a total of 720 observations (10 illuminations \times 24 color samples \times 3 repeats) were recorded. The mode was defined as a color name reported at least two times within the three repeats. Data analysis was performed on the modal responses of the three repeats for an observer for each color sample. Color samples without a modal response (i.e., the observer reported three different color names on the three repeats) were excluded. Consequently, 6% (61 of the 960 combinations) of illumination \times color sample \times observer was excluded because of a lack of consensus.

Results

Fig. 1 (lower panels) shows the reported color of the eight OSA-UCS color sample categories on the abscissa as a function of the illuminance (log Lux) on the ordinate, with one panel displaying one color sample category. Each symbol indicates the modal response of the three repeats for each participant at each illumination (see Fig. 1 legend for details). Because the samples at the three highest illumination levels were consistently reported in accordance with the basic color category names, Fig. 1 (lower panels) shows only results with illuminances from 0.0-3.5 log Lux.

With decreases in the illumination level, the reported color names of the OSA-UCS color samples fall into three domains, which differed from the color names employed at higher illumination levels. The categories employed are consistent with the idea that the color categories were based on the activity of rods and L-cones (Fig. 1, upper center panel). Samples with high longwavelength spectral content continued to be classified as red or orange, but the color identifiers for many of the other samples changed, with predominant use of the categories blue, blue-green, green, gray (as a descriptor, we term this the blue-green-gray category), and not detectable (we term this the black category). At the lowest three light levels, many samples with the highest long-wavelength content, especially red samples, were below threshold and were called black. The remaining suprathreshold samples were reported with color terms related to relative scotopic lightness. The colors of the shaded areas on Fig. 1 (lower 8 panels) depict the color terms used at the three lowest light levels; the samples identified as blue, blue-green, green or gray (and occasionally yellow) are shown by the shaded blue-green area, the

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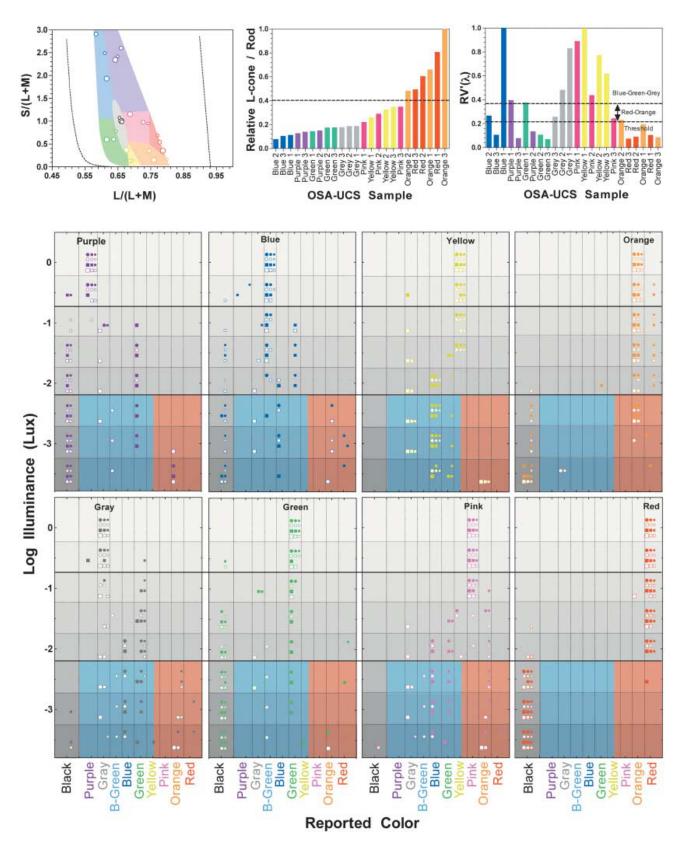


FIGURE 1

samples identified as red or orange are shown by the shaded red region. The samples below threshold, reported as black, are shown by the gray shaded region.

As an example of the changing hue percepts with decreasing illumination, the reported color names for the OSA-UCS "gray" samples in the left column of the lower panels of Fig. 1. For the three highest illumination levels (equal to or greater than $-0.5 \log$ Lux), all observers reported the hues of the samples as gray, which is their photopically assigned color (data for 0.5 and 1.0 log Lux not shown). At intermediate light levels (-1.0 to $-2.0 \log Lux$), the gray samples did not necessarily appear achromatic. Other than gray, reported hues included blue, green, and blue-green. For illuminations less than or equal to $-2.5 \log Lux$, reported hues for the OSA-UCS gray samples could be primarily classified into two hue categories that correlated with relative sample scotopic luminance: blue-green-gray and red-orange. Stimuli below threshold were reported as black. With few exceptions, the blue-green color names were assigned to the Gray-1 (largest symbols) and Gray-2 (medium size symbol) samples that have a high relative scotopic luminance (See Fig. 1, upper right panel). The Gray-3 sample (smallest symbol) has the lowest reflectance among the three gray samples. Again, with few exceptions, gray samples of low reflectance that were above rod threshold were reported as red-orange.

The same trends are observed for the other seven OSA-UCS color sample categories. The reported colors for all color samples are consistent with their photopic names at illuminations equal to or greater than $-0.5 \log Lux$. At intermediate illumination levels $(-1.0 \text{ to } -2.0 \log Lux)$, the reported colors are either close to their photopic colors, or are blue-green-gray, or black. The assigned color categories are consistent with rod and L-cone receptor input. The horizontal line on Fig. 1 (upper center panel) shows the approximate separation of samples with high and low L-cone excitation. The high L-cone excitation samples were generally identified as red or orange, the low L-cone excitation samples as blue-green-gray, or black.

At the lowest illumination levels $(-2.5 \text{ to } -3.5 \log \text{Lux})$, the reported colors can be associated with the relative scotopic luminance for the samples: samples seen as blue-green-gray are predominantly associated with high relative scotopic luminance, samples seen as red-orange are associated with intermediate relative scotopic luminance values, and samples reported as black are

assumed to have relative scotopic luminance below threshold. The dotted horizontal lines in Fig. 1 (upper right panel) indicate the approximate transitions between these color appearance regions. It is evident from the data in the lower panels that the transition region is variable and dependent on sample chromaticity, sample reflectance, and light level. Thus, it is not possible to represent the transition between cone and rod mediated (mesopic) and rod mediated (scotopic) vision by a single light level.

Taking into consideration the data for all illumination levels, modes could not be calculated because of a lack of consensus for 6% of the conditions. The $-1.0 \log$ Lux illumination level proved to be the light level having the greatest number of samples not showing consensus; at this light level 20% of the samples were given different color names in the three sessions. This illumination level lies at the transition between the higher light levels where the observers employed photopic color names and the intermediate light levels where the rods and the three cone types may mediate color percepts. Interestingly, consensus at the three lowest light levels, where vision was presumably mediated solely by rods, was better than at higher light levels where both rods and cones mediated percepts with 2%, 12%, and 4% of the low-light conditions failing to produce modes.

In Control Experiment 1, the observers reported hues for isolated color samples in the absence of contextual cues at the lowest illumination level ($-3.5 \log Lux$). Each of the suprathreshold samples was identified as blue-green. Therefore, we term the red-orange hue observed at low illumination levels with other samples in the field of view as "relational red-orange" (reddish shaded area on Fig. 1, lower panels). Control Experiment 2 assessed whether short term experience of a broad gamut of hues at the high and intermediate light levels might have contributed to the hue percepts seen at low light levels where only the rods were above threshold. The entire experiment was repeated with the omission of the samples appearing pink, orange and red at photopic levels. As anticipated, the descriptors associated with longwavelength stimuli were not used at the higher light levels. At the lower light levels each of the four observers identified some of the samples as red or orange. This is the same result as in the main experiment, indicating that photopic color identification experience was not responsible for the use of long-wavelength descriptors for some samples at the three lowest light levels.

Fig. 1. The top three panels represent the hypothesized photoreceptoral complement under decreasing illumination (left to right). The chromaticity coordinates for the 24 OSA-UCS samples in the cone chromaticity space (Cao et al., 2005a) are shown in the upper left panel. The shaded areas represent the Boynton and Olson (1987) eight basic non-contrast color regions. The dashed line shows the spectrum locus. The upper center panel shows the relative L-cone/Rod value of the samples. The color samples on the abscissa are ordered based on the relative L-cone/Rod values. The dashed line shows the approximate transitional ratio between samples with high and low L-cone excitation at the intermediate illumination levels $(-1.0 \text{ to } -2.0 \log \text{ Lux})$. The upper right panel shows the relative scotopic luminance of the samples. The color samples are ordered on the abscissa as in the upper center panel. The upper horizontal line indicates the approximate transition between the reported blue-green-gray and red-orange color names under scotopic conditions. Samples below the lower horizontal line were below threshold. The lower eight panels show the reported color of the eight OSA-UCS color sample categories (abscissa) as a function of photopic illuminance (ordinate) with one panel for each color sample category. The symbol size refers to the lightness of the OSA-UCS sample, with the smallest symbols representing the lowest lightness, and the largest symbols the highest lightness as specified in Table 1. Observers: filled circles () AJZ; unfilled circles (), DC; filled squares (), JP; unfilled squares (D), ML. The leftmost column in each panel shows samples reported as black (below detection threshold). The thick horizontal lines (-0.75 and -2.25 log lux) approximate the transition regions between the reported color domains with reduction in illuminance levels. The upper solid line $(-0.75 \log lux)$ demarcates the approximate transition from cone to rod and cone mediated color vision for stimuli reflecting predominantly short-wavelength radiation. The lower solid line $(-0.75 \log lux)$ approximates the illumination in which rods solely mediate hue percepts. The colors of the shaded areas at the three lowest light levels delineate the color categories used by the observers; blue-green-grey and red-orange. The samples below threshold (shaded gray) are coded as black.

Discussion

The major findings of the investigation can be summarized as follows: (1) there were salient and diverse color appearances at all illumination levels; (2) transitions between different receptormediated percepts depended on the sample chromaticity, reflectance and light level; and (3) at the three dimmest light levels, with multiple samples in the field of view, there were variegated hue percepts mediated by a single receptor system, the rods.

We found two categories of color appearance and names for light levels below the levels where the reported colors were consistent with the photopic identifiers. Except for the three lowest light levels where only rods function, there was a clear division in color appearance between samples predominantly reflecting longer wavelengths and the other visible samples. Rods and L-cones presumably mediated these percepts. An intuitive way to see this is to consider the color categories reported for the gray samples. If the percepts had been mediated by the L- and M-cones at light levels where the S-cones were below threshold, the expected response category would have been yellow because the spectral tritan metamer (wavelength producing the same relative excitations of the L- and M-cones) for the 5000 K light source is about 570 nm. The yellow category was not used by any of the observers; the reported color categories were reported green or blue or gray.

At the three lowest light levels, color appearance was generally associated with relative sample scotopic lightness (Fig. 1C, shaded areas). Under these conditions, a relative scotoma forms corresponding to the fovea centralis, and an observer unconsciously shifts fixation to a paracentral retinal location (Simon, 1904). Thus, with free fixation, as is the case in our experiment, the retinal location used for color judgments presumably shifted with light level. In accordance with the scotopic luminous efficiency function, in a dim natural environment, the objects with predominantly short- and medium-wavelength composition appear brighter, and objects with longer wavelength composition appear dimmer. Control Experiment 1 indicated that the scotopic color percepts are relational (i.e., at the lowest light level); some of the visible samples when presented in the context of the other samples were identified as red or orange, whereas when presented individually each was identified as blue-green. This is in accord with literature reports that rod color under scotopic and mesopic conditions may be blue, blue-green, or green (Cao et al., 2005b; for review see Nagel, 1924; Buck, 2004). Rods can also signal a diversity of hues in the presence of cone induced simultaneous and successive contrast, and in Mondrian patterns in which rods and L-cones mediate vision (McCann & Benton, 1969). Our results extend these reports in showing that even in the absence of cone contributions; various color percepts can be observed.

Given developmental and long-term experience with viewing familiar objects in the natural environment under dim illumination, an observer's visual system may infer that bright appearing objects are richer in short wavelength light compared to dim appearing objects. What is striking in our study is that all four observers noted conspicuous relational hues associated with high or low reflectance stimuli when they appeared contextually on the viewing surface. We speculate that with input solely from rods, and when confronted with an array of objects differing in scotopic lightness, the visual system estimates probable colors based on natural visual experience.

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References

- ASTM. (1994). Standards on Color and Appearance Measurement. Philadelphia: American Society for Testing and Materials.
- BOYNTON, R.M. & OLSON, C.X. (1987). Locating basic colors in the OSA space. Color Research and Application 12, 94–105.
- BROWN, W.R.J. (1951). The influence of luminance level on visual sensitivity to color differences. *Journal of the Optical Society of America* 41, 684–688.
- BUCK, S.L. (2004). Rod-cone interactions in human vision. In *The Visual Neurosciences*, eds. CHALUPA, L.M. & WERNER, J.S., pp. 863–878. Cambridge, MA: MIT Press.
- CAO, D., POKORNY, J. & SMITH, V.C. (2005a). Associating color appearance with the cone chromaticity space. *Vision Research* 45, 1929–1934.
- CAO, D., POKORNY, J. & SMITH, V.C. (2005b). Matching rod percepts with cone stimuli. *Vision Research* **45**, 2119–2128.
- CIE. (1951). Proceedings 1951, Vol. 3, p. 37, Paris: Bureau Central de la CIE.
- HECHT, S. & HSIA, Y. (1945). Dark adaptation following light adaptation to red and white lights. *Journal Optical Society of America* 35, 261–267.
- ISHIDA, T. (2002). Color identification data obtained from photopic to mesopic illuminance levels. *Color Research & Application* 27, 252–259.
- KOHLRAUSCH, A. (1931). Tagesehen, Dämmersehen, Adaptation. In Handbuch der Normalen und Pthologischen Physiologie, eds. BETHE, A., BERGMANN, G.V., EMBDEN, G. & ELLINGER, A., pp. 1499–1594. Berlin: Springer.
- KUEHNI, R.G. (2003). Color Space and Its Divisions, pp. 1–408. New York: Wiley-Interscience.
- MACADAM, D.L. (1978). Colorimetric Data for samples of OSA uniform color scales. *Journal of the Optical Society of America* 68, 121–130.
- MCCANN, J.J. & BENTON, J.L. (1969). Interaction of the long-wave cones and the rods to produce color sensations. *Journal of the Optical Society* of America 59, 103–107.
- MIDDLETON, W.E.K. & MAYO, E.G. (1952). The appearance of colors in twilight. *Journal of the Optical Society of America* 42, 116–121.
- NAGEL, W. (1924). Appendix: Adaptation, Twilight Vision and the Duplicity Theory. In *Helmholtz's Treatise on Physiological Optics Translated* from the Third German Edition by JPC Southall, Third German Edition, Vol. 2, pp. 313–343. Rochester, NY: Optical Society of America.
- PURKINJE, J. (1825). Beobachtungen und Versuche zur Physiologie der Sinne. Neue Beiträge zur Kenntniss des Sehens in subjectiver Hinsicht, pp. 1–192. Berlin: Reimer.
- SCHNEIDER, N. & VON CAMPENHAUSEN, C. (1998). Color and lightness constancy in different perceptual tasks. *Biological Cybernetics* 79, 445–455.
- SHIN, J.C., YAGUCHI, H. & SHIOIRI, S. (2004). Change of color appearance in photopic, mesopic and scotopic vision. *Optical Review* 11, 265–271.
- SIMON, R. (1904). Über Fixation im Dämmerungssehn. Zeitschrift für Psychologie und Physiologie der Sinnersorgane 36, 186–193.
- SMITH, V.C. & POKORNY, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. Vision Research 15, 161–171.
- VERRIEST, G., BUYSSENS, A. & VANDERDONCK, R. (1963). Etude quantitative de l'effet qu'exerce sur les resultats de quelques tests de la discrimination chromatique une diminution non selective du niveau d'un eclairage c. *Revue d'Optique* 3, 105–119.
- WALD, G. (1945). Human vision and spectrum. Science 101, 653-658.
- WALKEY, H.C., BARBUR, J.L., HARLOW, J.A. & MAKOUS, W. (2001). Measurements of chromatic sensitivity in the mesopic range. *Color Research & Application* 26, S36–S42.