

Herrick defines the auricle as "composed of tissue which is transitional between the body of the cerebellum and the acoustico-lateral area of the medulla oblongata. This auricle contains the primordia of the vestibular part of the cerebellar cortex. . . ."

Finally, the premammalian nucleus cerebelli appears, in mammals, to become "subdivided and incorporated within the cerebellar mass as the deep nuclei" (3).

That vestibular cortex of the mammalian cerebellum has the direct output and partially direct input lines just described may be an arrangement of some antiquity that has survived for adaptive reasons because it favors rapid computation, or rapid adjustment, of the body's position in space.

Appropos that point, Turkewitz and Kenny (4) note that in newborns "the sequence of functional onset—vestibular, cutaneous, olfactory, auditory and visual, is invariant across all species of birds and mammals thus far studied."

What Hockfield's study suggests is that monoclonal antibodies may in some instances be used to label neuronal subpopulations according to their phylogenetic age. Characterization of this type might be of particular interest in structures such as the dentate gyrus, in transitional areas such as entorhinalis, or in parts of association cortex defined by Graybiel (5) as "distal."

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Response: Fair states explicitly an implication of my observation that antigenic differences correlate with anatomical and functional differences among neurons in the rat cerebellum. The functional properties of neurons are presumably derived, like other cellular characteristics, through the selective evolutionary retention or loss of specific molecular species. One might then predict that the isolation of cell specific markers could reveal functional characteristics that reflect phylogenetically conserved properties.

While we have not yet tested Fair's predictions in the systems he describes, our results

in another system (1) suggest a phylogenetic conservation of molecular expression to a functional class of neuron. Monoclonal antibody Cat-301 recognizes functionally defined neuronal subsets in the feline and primate dorsal lateral geniculate nucleus (LGN). The cellular organization of the LGN is quite different in cat and in monkey, yet the Cat-301 antigen is expressed by functionally equivalent neurons in both animals irrespective of their distribution or nearest neighbor relationships. These results indicate that some molecular properties of neurons may be phylogenetically conserved by functionally related neurons. The conser-

vation of molecular traits could be useful in identifying homologous neuronal populations when differences by cytoarchitecture, physiology, or connections might obscure evolutionary relationships.

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Color Vision and the Retinex Theory

D. J. Ingle (1) presented evidence for color constancy and the Retinex theory of Land (2) in goldfish. From the results of one experiment, he concluded that fish can discriminate "a green paper whose spectral distribution of reflected light was identical to that of the gray paper." That is, papers of different spectral reflectances must look different even when illuminated so they reflect identical light spectra, a result impossible to explain by means of colorimetry. However, the methods in such Retinex experiments equate only the integrated light of spectral distributions, not the spectral distributions themselves, as Ingle stated. Hence virtually any detector other than the specific detector used for the match could still respond differentially to the "equated" papers.

On each side of the match is a projector passing light through a band-pass filter with transmission spectrum $\tau(\lambda)$. The projector sending light to a paper with chromatic reflectance $\rho_1(\lambda)$ is equipped with a tungsten light bulb at temperature T_1 , and the projector sending light to a paper with another chromatic reflectance $\rho_2(\lambda)$ has a tungsten light bulb at temperature T_2 . Given that the lighting and viewing geometries are the same for both projectors and for both reflectances, the lights entering the eye from the two papers have spectral power distributions

$$\begin{aligned}\phi_1(\lambda) &= b(\lambda, T_1)\tau(\lambda)\rho_1(\lambda) \\ \phi_2(\lambda) &= b(\lambda, T_2)\tau(\lambda)\rho_2(\lambda)\end{aligned}\quad (1)$$

where $b(\lambda, T)$ is the spectral distribution of tungsten as a function of temperature.

A light meter with spectral sensitivity $S(\lambda)$ is then used to adjust T_1 so that when the projector illuminates $\rho_1(\lambda)$, the light meter registers a match to the integrated light received from $\rho_2(\lambda)$:

$$\int \phi_1(\lambda)S(\lambda)d\lambda = \int \phi_2(\lambda)S(\lambda)d\lambda \quad (2)$$

An artifact arises from the fact that the filters $\tau(\lambda)$ have a spectral bandwidth (that is, they are not monochromatic). As a result, Eqs. 1 prove that the spectral distributions $\phi_1(\lambda)$ and $\phi_2(\lambda)$ reaching the eye must be different because (i) $\rho_1(\lambda)$ has a different spectral shape from that of $\rho_2(\lambda)$; and (ii) the illuminant spectrum $b(\lambda, T)$ depends on T , which is different for $\phi_1(\lambda)$ and for $\phi_2(\lambda)$.

The match of Eq. 2 therefore holds only

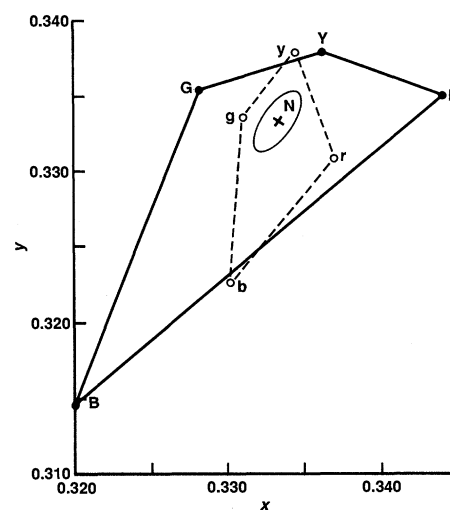


Fig. 1. Chromaticity coordinates for blue (b, B), green (g, G), yellow (y, Y), red (r, R), and neutral (N) test papers with identical triplets of light meter readings for 50-nm (solid line) and 10-nm (dashed line) bandwidth spectral filter Retinex illumination conditions. For the 50-nm filter condition (filled circles), the "equated" papers show a total variation about 22 times the area of the nearest MacAdam ellipse (3). [The nearest ellipse is at $(x, y) = (0.305, 0.323)$, but is centered at the neutral reflectance for easy visual comparison.] For the 10-nm condition (open circles), the variation is less than for the 50-nm condition, but it is still about eight times the area of the MacAdam ellipse. Any chromaticities outside the bounds of the MacAdam discrimination ellipse shown would be discriminable from neutral by a human.

for detectors with spectral sensitivities proportional to $S(\lambda)$, or orthogonal to ϕ_1 minus ϕ_2 . A detector with any other spectral sensitivity must respond differentially to the two papers, which allows for a potentially easy discrimination.

An additional artifact is that the matching procedure used in Retinex experiments equates only light meter readings, not radiances or energies as stated, since a correction is apparently not made for the spectral sensitivity curve $S(\lambda)$ of the light meter at each wavelength within the pass-bands of the filters.

It might still be stated that, although such artifactual spectral differences exist, they are too small to be detectable, but no Retinex experiment has yet been reported that describes the spectra of the light entering the eye. However, a computation based on a plausible realization of the experiments shows large artifactual effects.

For the illuminant $b(\lambda, T)$, I used the blackbody spectrum (3, p. 14), corrected for the emissivity of tungsten (interpolated from 3, p. 16). Ingle (1) did not specify the filters he used. I therefore assumed they were the standard 50-nm bandwidth filters used in Land's Retinex experiments (2). To investigate the effect of filter bandwidth, I also used the 10-nm bandwidth filters of McCann *et al.* (4), assuming exponential falloff from the peak transmittance.

Ingle also did not specify the paper reflectances. I therefore chose the 14 test samples recommended by the International Commission on Illumination (CIE) for calculating color-rendering indexes (5, pp. 473–474) and a "neutral" patch with constant 50% reflectance. These are likely to encompass the range of papers used by Ingle. The light meter used in Land's Retinex experiments has an S-11 photosensitive surface (2), for which a typical spectral curve has been published (6). The values of T_2 were set so that the chromaticity coordinates (x and y) of the neutral gray paper were 0.3333 and 0.3333, respectively. With these known functions and values (none of which were critical except filter bandwidth) it was then possible to compute T_1 with the use of a successive approximation procedure so that Eq. 2 was satisfied for any filter and paper. Calculations were carried out to 14 decimal places, from 380 to 700 nm at 10-nm intervals, and all matches were made to the sixth decimal place or more. The final T_1 values were within the standard tungsten range of 2150 K to 3450 K (6). These procedures determined completely $\phi_1(\lambda)$ and $\phi_2(\lambda)$. The CIE tristimulus values of the reflected light from the "strong" hues in the set of 14 reflectances (3, p. 174) are plotted in Fig. 1 for the 50-nm and 10-nm filter

conditions.

Figure 1 shows that "identical" reflected lights, although constrained to match radiometrically according to the Retinex criteria, are still different enough to be easily discriminable in chromaticity by a human. Goldfish chromatic discrimination capabilities have yet not been adequately tested, but the available data (7) indicate that their wavelength discrimination capabilities are sufficiently close to those of humans that such large chromatic differences should also be discriminable by them. Furthermore, as seen in Fig. 1, the variations turn out to be in just such directions that the object-color hues can be determined directly from the chromaticity space without the need for Retinex processing.

Equally large and generally even larger chromaticity differences were found with the use of (i) other published $S(\lambda)$ curves, (ii) other sets of Munsell reflectance curves, (iii) radiance values corrected for the spectral sensitivity of the radiometer at each wavelength in the pass-bands of the filters, (iv) other chromaticities of the neutral point, or (v) neutral density filters rather than variations of color temperature to vary intensity. The only way I found to limit the magnitude of the artifacts was to reduce the spectral bandwidth of the illuminants. With monochromatic illuminants (bandwidth = 1 nm) the artifacts vanished completely—all the papers became chromatically identical to neutral.

Land (8) used monochromatic lights in some early color experiments, but not with the Retinex experimental paradigm. Also, the single-element Littrow monochromators (3, p. 66) he used are prone to stray light and higher order spectral artifacts (3). No Retinex experiments have yet been reported with controlled monochromatic lights.

This analysis suggests that some refinements and controls are needed in the Retinex experiments before they can be truly said to demonstrate that identical stimuli can produce different responses (9).

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9. The scope of this comment is limited to stimuli "equated" by means of the Retinex methodology. I do not maintain, nor do these results indicate, that the wavelength-energy distribution reaching the eye can always explain perceived hue under other, non-Retinex viewing conditions. Likewise, these results say nothing about the validity of the Retinex theory per se; it is shown only that the Retinex theory is not needed to explain Retinex data for "equated" stimuli. However, the scope of the comment does extend to the "equated" paper results in all Retinex experiments conducted to date, as well as to all alternative explanations of such results by other investigators who have used different color theories, who likewise appear to have overlooked the artifacts raised here.
10. I thank Michael H. Brill for insightful discussion.

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Response: Young suggests that two colored papers we presumed to be "equated" for spectral reflectance are not sufficiently equated and may thus be perceived by a fish as being of different colors. The main point of a color constancy demonstration, however, is that areas with vastly different spectral characteristics look "the same" to the goldfish, as to the human observer. At the same time we showed that our equated papers can look very different: for example, they can appear as green, gray, or even yellow, depending on the nature of the surrounding array of colors. Young does not tell us how different his "replications" of our equated colors actually look to a human observer. In Land's experiments equated patches look the same when viewed against a dark background, but suddenly change to different colors when a complex colored background is added. So the differences in color that are to be explained by Retinex theory are not evident in the spectral differences between areas when the colors are viewed against a dark background.

Young uses the response curve of an uncorrected S-11 photomultiplier tube as the basis of his computations. A meter with this tube was used in some of Land's earlier work, but was nevertheless equated for equal energies. The references and notes from our paper specifically mention the Spectra-Prichard 1980A. This photometer has a specially selected S-20ER photomultiplier tube and is used in conjunction with a radiometric filter designed to produce a spectral response that is relatively flat from 450 nm to 700 nm. This total system greatly reduces any effect contributed by the spectral distribution of the band-pass filters specified.

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