Reports

Red − Green Opponent Spectral Sensitivity: Disparity Between Cancellation and Direct Matching Methods

Abstract. *The spectral sensitivity at the opponent stage of the visual system is traditionally measured by a hue-cancellation procedure. Comparison with a direct hue-matching method shows that cancellation overestimates short-wavelength sensitivity by as much as a factor of 30. The observation implies that different mechanisms control the perception of short-wavelength and long-wavelength redness.*

According to recent theories of color vision, the signals from three kinds of cones are transformed to sum and difference signals (*1–3*). Figure 1 shows a conventional diagram of the transformations of the cone spectral sensitivities into one achromatic, or sum, signal and two chromatic, or difference, signals. The sum signal, $L + M = V_\lambda$, is usually considered to be the luminance signal. The two difference signals, $r - g$ and $y - b$, are wavelength-dependent and carry information about hue. Although estimates of the spectral sensitivities of the cones have been published recently (*4*), knowledge of the transformed sensitivities has advanced little since Judd's 1951 summary (*5*).

The method for directly measuring the spectral sensitivities of the color opponent channels in humans takes advantage of the opponency. The amount of, for example, redness at a given wavelength is measured by how much of the opponent hue, green, is required to cancel it. To measure the spectral sensitivity of the $r - g$ channel, either of two primaries (for simplicity, a unique red or a unique green) is added to unit amounts of spectral test wavelengths to cancel the greenness or redness from the mixture. The amount of the red primary required to cancel the greenness from a 550-nm test defines how much green is in the 550-nm test. The method produces curves for the spectral sensitivities of the opponent stage similar to those shown in the opponent boxes of Fig. 1.

The validity of the cancellation procedure for measuring spectral sensitivity may itself be suspect; the procedure itself may alter the spectral sensitivity of the channels. There is evidence that adding a desaturant (light from a different region of the spectrum) or maintaining light adaptation affects the spectral sensitivity of the opponent channels at short wavelengths (*6, 7*). Because the cancellation method necessarily desaturates the test light, a mechanism sensitive to saturation may change the resulting spectral sensitivity.

To test the validity of the cancellation procedure requires a method of estimating the amount of hue present in an equal-luminance test spectrum in a way that does not desaturate the test spectrum. The most straightforward way is for the observer to match the amount of hue present by using the same primaries to make a comparison as are used for the cancellation. Figure 2A shows the $r - g$ spectral sensitivities measured with the cancellation method and a direct comparison, or hue-matching, method. To obtain the matching curve, first a 400- to 700-nm test spectrum was flicker-matched at 10-nm intervals to a 100-troland standard to develop an equal-luminance spectrum. This test spectrum covered the left half of a 5° bipartite field. Then the subjects matched the amount of redness or greenness perceived in the test spectrum by adjusting two primaries that were mixed on the right side of the field. These primaries (except red) (*8*) were the unique hues for the two subjects and were the spectral lights 680 and 480 nm for the spectral region 400 to 480 nm, 480 and 520 for 480 to 520 nm, 520 and 580 for 520 to 580 nm, and 580 and 680 for 580 to 680 nm. Besides setting the primary mixture so that it appeared to contain the same amount of redness or greenness as the test side, the observer also adjusted a neutral density wedge common to both primaries to make the mixture of primaries match the brightness of the test side. The amounts of the primaries set by the subject were measured at the exit pupil of the four-channel Maxwellian view with a calibrated photomultiplier tube.

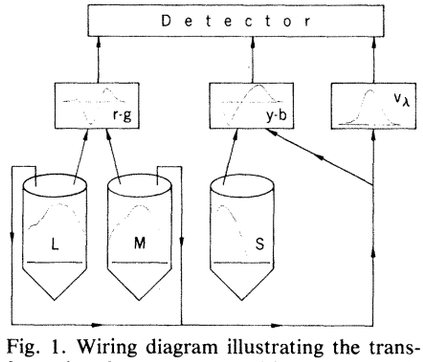

Fig. 1. Wiring diagram illustrating the transformation from cones sensitive to long (L), medium (M), and short (S) wavelengths (*4*) to the difference and sum signals found at later stages. The transformation equations for the $r - g$ (red − green) channel are given in the text. The transformation equations for the other two channels, neglecting coefficients, are $V_\lambda = L + M$ and $y - b = V_\lambda - S$ where V_λ is the relative luminosity function and y and b represent yellow and blue. The curves shown in each box represent the spectral sensitivity of the labeled process.

To obtain the cancellation curve, subjects added either green (520 nm) or red (680 nm) primary to the proper region of the 100-troland test spectrum until it was neither reddish nor greenish (*9*).

Because the same 100-troland test spectrum and the same primaries were used for both the matching and cancellation curves of Fig. 2A, a single convention normalizes the different parts of each curve, and each curve with respect to the other. Let 100 trolands be one unit of the green primary, and one unit of the red primary be that amount required to cancel it. The amounts of the primaries required to cancel the equal-luminance test light were converted to spectral sensitivities by multiplying them by the subject's own flicker spectral sensitivity measured at 100 trolands.

The cancellation and matching techniques agree closely except for the violet region of the spectrum, from 400 to 480 nm (Fig. 2A). In this region, the cancellation method indicates that there is about 30 times more redness than the comparison method. Thus, the use of a desaturant greatly increases the sensitivity of the $r - g$ opponent stage at short wavelengths. In our view this effect is re-

Scoreboard for Reports. The acceptance rate for Reports during the last year has been about 25 percent. The number accepted has exceeded the number published and publication delay has increased to about 4 months. For the next few months, our acceptance rate will be about 15 percent, or ten Reports per week.

0036-8075/78/0929-1221$00.50/0

lated to the Abney effect (*10*), in which a white light desaturant increases the redness of violet lights. A green light is as effective as a white light in producing additional redness (Fig. 2A). However, because the green light also cancels redness, the hue change is not directly observable. In a separate experiment, we have measured the amount of green light required to cancel the redness in a violet field and also to cancel the redness in a mixture of 680 and 480 nm which matches (for redness) the violet field. It takes at least ten times more green light to cancel the redness from the violet than it takes to cancel the matching redness from the comparison field, independent of the intensity from 0.5 to 500 trolands. Thus a canceling green primary light, added to a violet test near 420 nm, produces nine-tenths as much redness as it cancels, and hence, ten times as much green light must be added to cancel a unit of redness at 420 nm as must be added to cancel a unit of redness at the long wavelength end of the spectrum.

A theory of this effect based on the "silent surround" reported in single unit recording of receptive fields of the lateral geniculate nucleus in the primate (*11*) has been proposed (*7*). Surrounds are characterized as silent if, when stimulated alone, they produce no change in ganglion cell–firing rate but nonetheless can be shown to have an effect by inhibiting an active center (*11*). For simple opponent cells, which have different spectral sensitivities for centers and surrounds, a desaturant—that is, light from a spectral region to which the center is sensitive—is necessary before the presence of the surround becomes apparent. In other words, silent surrounds do not signal unless there are active centers to inhibit. To express this concept quantitatively, define an operator, Θ, such that $a \Theta b = a - b$ when $a > b$ and zero when $a < b$. Hypothetically, S cones lie in the surrounds of $M - S$ receptive fields but are silent unless $M > S$. Figure 2A also shows a comparison of two theoretical spectral sensitivity curves, calculated by normalizing the cone spectral sensitivities to produce neutral points at 480 and 580 nm. The Θ operator model for silent surrounds agrees well with the data.

The transformation of the cone spectral sensitivities L, M, and S to the $r - g$ opponent spectral sensitivity is $r - g = -(1.481\ M - 0.428\ S - L)$ for the dotted curve and $r - g = -(1.481\ M \Theta 0.428\ S - L)$ for the solid curve. The silent-surround hypothesis can be used to predict $r - g$ spectral sensitivity by noting that for the cancellation method the field is always desaturated. This means that the center of the receptive field is active, so the surround can inhibit the center; the surround sensitivity subtracts from the center sensitivity ($M \Theta S = M - S$). Thus, for the cancellation condition, $r - g = -(1.481\ M - 0.428\ S - L)$. The coefficients in this equation are determined because the zero crossings of the $r - g$ curve must lie at the correct unique hues, and there are no free parameters that can be adjusted to make the theory fit the data. In the matching procedure, the spectral hues are not desaturated; for wavelenghts where $0.428\ S$ is larger than $1.481\ M$, the signal from $M \Theta S$ receptive fields becomes zero and the spectral sensi-

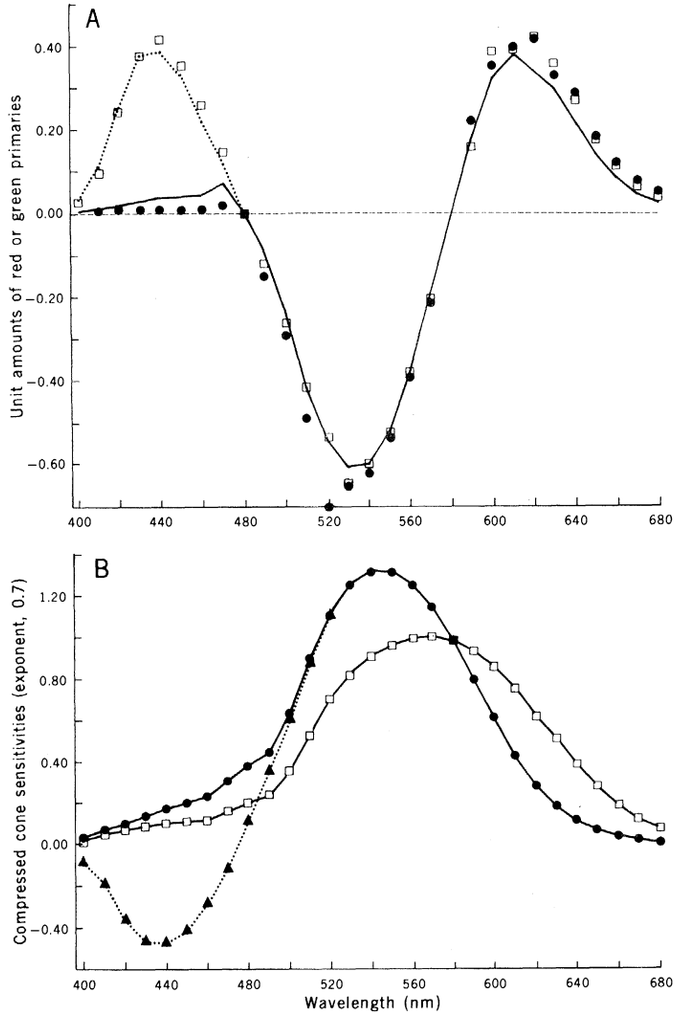

Fig. 2. (A) Comparison of matching and cancellation curves. The square symbols show the units (adjusted as described in text) of green primary (above the dashed line) and red primary (below the dashed line) required to cancel the redness or greenness from 100-troland spectral test lights. The circles show the amounts of the same red and green primaries required to match the redness or greenness in the same test spectrum. The solid line curve and the dotted curve, which are identical from 480 to 680 nm, are theoretical curves for the cancellation and matching conditions, respectively, calculated from the transformation equations given in the text. The data shown are from a single typical run by observer C.R.I.; data from observer P.W.R. are similar. (B) The spectral sensitivities of the L (□) and M (●) cone pigments normalized to produce a neutral point at 580 nm. For this normalization, M cones are more sensitive than L cones at short wavelengths, and hence, this system cannot signal $+r$ for wavelengths between 400 and 580 nm. The dotted curve, which is the difference $1.481\ M - 0.428\ S$, shows that the S cone must inhibit the M cone to produce the proper short-wavelength cross point at 480 nm. The ordinate is an exponential compression used to eliminate the discontinuity that occurs at zero with the more familiar logarithmic ordinate.

tivity reduces to L. This happens for wavelengths shorter than 480 nm. For wavelengths longer than 480 nm, the two equations are identical. The theoretical curves are plotted in Fig. 2B. The cancellation ($M - S$) equation is linear while the matching equation is not, which implies that the $r - g$ opponent spectral sensitivities are linear combinations of the cone pigments if measured under conditions for which the Θ fields do not become zero—that is, where the M centers are more responsive than the S surrounds.

This theory shows that adding green light to a violet field has opposite effects. The green light cancels the redness in the usual opponent sense. But green light also activates the silent S surrounds, which by opposing the M cone necessarily signal redness.

When the L and M cone sensitivities are normalized at the long-wavelength neutral point (Fig. 2B), L can never signal r at $\lambda < 580$. The M cone is always more sensitive than the L cone, so unless the S cone inhibits the M cone enough to reduce its sensitivity to less than that of the L cone, the L cone cannot produce the $+r$ signal on opponent spectral sensitivity curves at short wavelengths. Although for the Θ S curves the $+r$ sensitivity arises from the L cone, it is the inhibition of M by S that allows this $+r$ to appear at short wavelengths (*12*). This fact also explains why long-wave adaptations may decrease short-wavelength $+r$. From the viewpoint of opponent theory, any cones that inhibit M signal $+r$ regardless of their spectral sensitivity.

The transformation equations from cone to channel spectral sensitivities for the $r - g$ channel require two differencing mechanisms within the channel. One of these mechanisms opposes the L cone to the M cone, the other the S cone to the M cone. Comparing the results of a hue-cancellation experiment with a hue-matching experiment suggests that the two mechanisms have different properties. The difference computed by the $M - L$ mechanism is a true $r - g$ signal in the sense that the difference signifies redness or greenness, depending upon the polarity of the difference. The M Θ S mechanism apparently signals only redness; the difference is zero unless the output of the M cones is greater than that of the S cone.

CARL R. INGLING, JR.
PHILLIP W. RUSSELL
MARK S. REA
BRIAN H.-P. TSOU
Institute for Research in Vision and
Division of Sensory Biophysics,
Ohio State University, Columbus 43212

References and Notes

1. D. Jameson, in *Handbook of Sensory Physiology*, D. Jameson and L. M. Hurvich, Eds. (Springer-Verlag, New York, 1972), vol. 7, p. 537.
2. S. L. Guth and H. R. Lodge, *J. Opt. Soc. Am.* **63**, 450 (1973).
3. C. R. Ingling, Jr., and B. H.-P. Tsou, *Vision Res.* **17**, 1075 (1977).
4. J. J. Vos and P. L. Walraven, *ibid.* **11**, 799 (1971). The cone spectral sensitivities used for theoretical calculations in this report were tabulated by V. Smith and J. Pokorny (personal communication) and can be found in Ingling and Tsou (*3*).
5. D. B. Judd, in *Handbook of Experimental Psychology*, S. S. Stevens, Ed. (Wiley, New York, 1951), p. 811. Other recent work has converged on sensitivities resembling those in Judd's review [for example (*2*)].
6. J. R. Moeller, thesis, University of Michigan (1976).
7. C. R. Ingling, Jr., *Vision Res.* **17**, 1083 (1977).
8. Our red primary was not unique in that some yellow is present in a deep red 680-nm light; however, this is immaterial to the arguments.
9. To obtain greater accuracy, instead of using a reference white surround or matching field, the other side of the bipartite field was a mixture of the yellow (580 nm) and blue (480 nm) primaries. These primaries were adjusted to match the canceled side. Thus, to get a cancellation setting for the red or green primary required making a complete trichromatic color match. In a separate experiment, we verified that a mixture of the 480- and 580-nm primaries defines the locus in the chromaticity chart of hues that are neither reddish nor greenish. Therefore, making the color match ensures that the exact amount of red or green primary required to make the test side of the field neither reddish nor greenish has been added. This method is greatly superior to the usual method in reliability and precision.
10. G. Wyszecki and W. S. Stiles, *Color Science* (Wiley, New York, 1967), p. 564.
11. T. Wiesel and D. Hubel, *J. Neurophysiol.* **29**, 1115 (1966).
12. F. M. De Monasterio and P. Gouras, *Vision Res.* **17**, 1147 (1977).

1 March 1978; revised 14 June 1978

Toxicity in Resting Cysts of the Red-Tide Dinoflagellate *Gonyaulax excavata* from Deeper Water Coastal Sediments

Abstract. *For the first time,* Gonyaulax excavata *cysts have been shown to be toxic. Bottom sediments from a water depth of 90 meters off the Maine coast were extremely rich in cysts, which were approximately ten times more toxic than the corresponding motile stages. Cysts are probably ingested by shellfish, thereby causing shellfish toxicity in deeper waters offshore and contributing to shellfish toxicity in shallower coastal waters. A new approach to the problem of paralytic shellfish poisoning is therefore needed, one that takes into account benthic cysts and sedimentary factors affecting their distribution. The possible dangers of spreading poisoning through human activities must be considered.*

Paralytic shellfish poisoning (PSP) is a well-documented food poisoning (*1*, *2*) in which toxins produced by microscopic phytoplankters (dinoflagellates) are accumulated in shellfish and passed on to humans who eat the shellfish. At least 300 human fatalities are known to have been caused by PSP worldwide (*3*), and there is disturbing evidence that outbreaks are increasing in intensity and spreading to new areas (*3*, *4*). These outbreaks focus attention on the hazards to both public health and the fisheries industry and emphasize the need for extended monitoring and better forecasting programs. Earlier suggestions for developing forecasting programs have relied solely on the monitoring of dinoflagellate motile stages in the water column and on environmental factors contributing to their growth and distribution. We report here large concentrations of highly toxic dinoflagellate resting cysts in bottom sediments. The relationship between toxic dinoflagellate blooms and shellfish toxicity may therefore be more complicated than has been thought, and toxicity forecasting will need to include consideration of benthic cysts and sedimentary factors affecting their distribution.

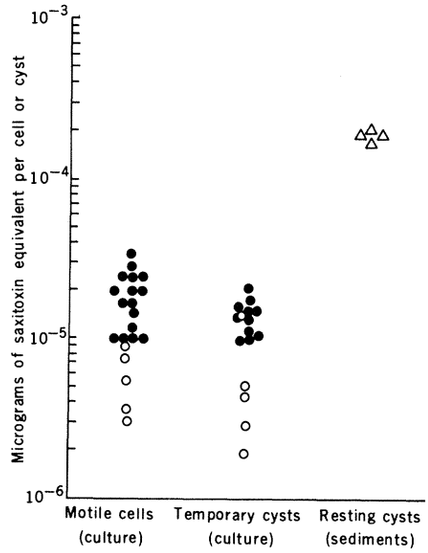

Fig. 1. Saxitoxin equivalent per cell or cyst for (○) motile cells or temporary cysts induced from logarithmic-phase motile cells in batch culture, (●) motile cells or temporary cysts induced from stationary-phase cells in batch culture, and (△) resting cysts estimated from sieved sediments.

Recently, temporary cysts and benthic resting cysts were described for the New England red-tide dinoflagellate *Gonyaulax excavata* (*5*). Prior to this work, benthic cysts were implicated as a likely cause of shellfish toxicity in deeper waters, even though no such cysts had been identified from either plankton or sediments (*6*). This implication was based on

0036-8075/78/0929-1223$00.50/0