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Red/Green Color Opponency at Detection Threshold

Abstract. *By means of visual stimulus without temporal or spatial edges, we have achieved better isolation of chromatic signals at detection threshold than has been reported previously. Under various states of adaptation, the spectral sensitivity of the chromatic mechanism detecting middle- and long-wavelength lights corresponds with that deduced from suprathreshold red/green hue equilibriums.*

The concept "color opponency" originated with Hering, who proposed that chromatic sensations occur along two independent, bipolar dimensions: red/green (R/G) and yellow/blue (Y/B) (*1*). Lights that cause neither sensation of an opponent pair are said to be in equilibrium with respect to that dimension. For example, equilibrium or unique yellow is the long-wave spectral light that appears neither reddish nor greenish. Hurvich and Jameson developed Hering's opponent process theory and applied it to a wide range of phenomena (*2*). Their hue cancellation procedure is the basis of quantitative opponent colors theory (*3, 4*). This procedure determines for each opponent system a subtractive coding of cone signals: the R/G (or Y/B) code assigns the value zero to a light if and only if that light is in R/G (or Y/B) equilibrium. Threshold experiments, which require no judgments of hue quality, have confirmed the existence of subtractive interactions between cone signals (*5–7*), but have not of themselves implicated the particular coding scheme hypothesized by opponent colors theory.

Figure 1 shows a series of spectral sensitivity curves. Curves A through C represent sensitivity to a novel test stimulus, and curve D is previously published data obtained with a conventional stimulus (*5*). The unique features of the new stimulus were its shape and time course: its temporal wave form was one period (trough-to-trough) of a 2-Hz cosine wave; its spatial profile was a radially symmetric Gaussian with a full bandwidth of 3°. This test will be dubbed the "low-frequency" test because its temporal and spatial Fourier spectra show that most of its energy is concentrated at low frequencies. Previous evidence indicated that chromatic visual channels are relatively more sensitive at low spatial and temporal frequencies, whereas achromatic or luminance channels are most sensitive at higher frequencies (*8*). The three bottom curves are estimates (*9*) of the spectral sensitivities of the three human cone pigments with peak sensitivities near 440, 540, and 570 nm (here labeled P_{440}, P_{540}, and P_{570}).

A notable feature of all the threshold spectral sensitivities is their peaks and troughs. Below 500 nm is a peak that can be attributed to P_{440} alone. Above 500 nm there are two peaks [or one shoulder and one peak (*10*)] whose location and bandwidth clearly do not correspond to those of the underlying cone spectra. These narrowed peaks have been attributed to linear subtractive interaction between the cones containing P_{540} and the cones containing P_{570} (*5*). An important quantitative feature of the new curves A through C is the magnitude of the troughs (arrows). Using the low frequency stimulus produced troughs more than twice as deep as that in curve D, the deepest trough previously reported for normal human observers.

Figure 2 shows another way to quantify the sensitivity loss revealed by the troughs in Fig. 1. Here curves B and D of Fig. 1 are transformed and replotted as equivalent threshold mixtures of two "primaries" (*11*). In the Rayleigh region of the spectrum (wavelengths longer than 540 nm) the normal eye is dichromatic: each spectral light in that region can be matched exactly (in photons caught by the cones) by a unique mixture of two spectral lights (primaries), one chosen from each extreme of the region. Plotted in this way, the data directly demonstrate a subtractive interaction of the signals generated by the two primaries: more of one primary necessitates more of the other to attain threshold. The topmost point for the low-frequency test shows that 6 times the threshold amount of 650 nm added to 3.5 times the threshold amount of 540 nm is just barely at threshold. To our knowledge, the inhibitory interaction revealed by the low-frequency test is more extreme than any previously observed in experiments measuring threshold for bichromatic mixtures with a more conventional stimulus (*6, 7*). The slopes of the linear portions of the threshold contours give the relative sensitivity of the detecting mechanism to the two primaries. The parallelism of the two sides of the low-

frequency threshold contour implies that the same linearly subtractive mechanism underlies detection on both parallel portions.

Curves A through C in Fig. 1 also exhibit a new, qualitative phenomenon: the minimum of the sensitivity trough is located exactly at the wavelength of the adapting background (arrows). If one assumes that the trough is due to a zero crossing in the response of a single linearly subtractive mechanism, the sliding of the trough's minimum to the adaptation wavelength corresponds to the sliding of this spectral crossover point. This form of adaptation could optimize chromatic discrimination under the ambient illumination conditions (*12*). This new phenomenon also provides a way to test the hypothesis that the subtractive mechanism responsible for detection is the same as that assumed by Hurvich and Jameson to account for suprathreshold R/G hue equilibriums. If they are the same, then both the sensitivity trough and R/G hue equilibriums are manifestations of the same zero crossing. Therefore the locus of unique yellow, like the sensitivity trough, should slide to the wavelength of the adapting background (*13*). This prediction was tested as follows.

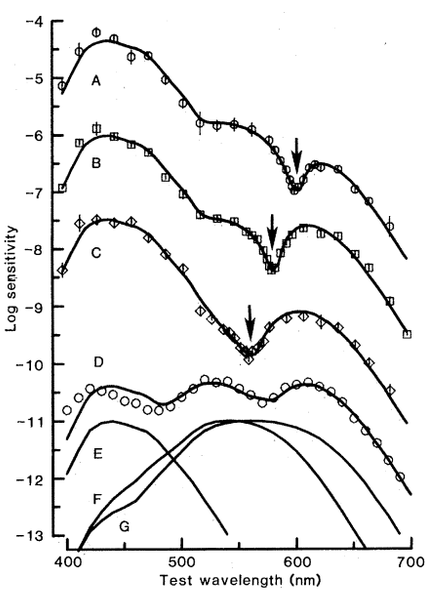

Fig. 1. (A–C) Threshold spectral sensitivity of the low-frequency test stimulus centrally fixated on ten backgrounds of 560, 580, and 600 nm (arrows) light at intensity $10^{10.0}$ quanta sec^{-1} deg^{-2} (7900, 6600, and 4700 trolands). The psychophysical procedure used to measure threshold was a two-alternative forced-choice staircase lasting 40 to 50 trials. Each plotted point is the mean of at least three such staircases measured on separate days. Error bars (which are usually smaller than the symbols) are ±1.0 standard error of the mean. Curve B is positioned absolutely in units of quanta sec^{-1} deg^{-2}; for clarity A and C have been shifted ±1.5 log units. Observer: R.M. (D) Data from Sperling and Harwerth [figure 4 in (*5*)]. Spectral sensitivity of a 45-minute (arc), 50-msec test on a 5500 K, white, 10,000-troland, 10° (arc) background. Solid lines A through D are the fits of the model described in the text. (E–G) P_{440}, P_{540}, and P_{570} photopigment spectra from Vos (*9*).

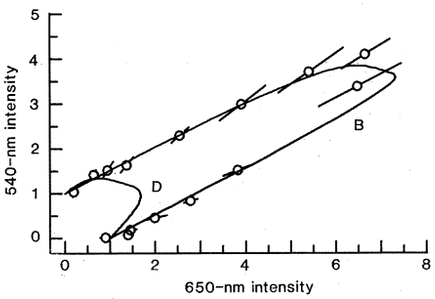

Fig. 2. Spectral sensitivities *B* (data and model) and *D* (model only) from Fig. 1 transformed with CIE color matching functions into matching mixtures of 650- and 540-nm light. The unit on each axis is the threshold amount of that primary by itself.

We measured a spectral sensitivity function with the low-frequency test stimulus (open symbols in Fig. 3). These threshold measurements were obtained with a forced-choice procedure that entailed no judgment of color quality. Next, on the same adapting background and again with the low-frequency stimulus, we found the locus of spectral unique yellow (closed symbols in Fig. 3). Due to apparatus limitations, it was necessary to use adapting field intensities 1.0 log unit lower than those in Fig. 1 in order to obtain a large suprathreshold intensity range over which to measure unique yellow. Although the threshold sensitivity trough was not so deep on these less intense fields (*14*), it was still well defined. The prediction was sustained: both the minimum of the sensitivity trough and unique yellow shifted to the wavelength of the background, so that a single vertical line through the trough separates the long-wave threshold peak and the suprathreshold reddish appearing lights from the mid-wave peak and greenish appearing lights.

To formally analyze the sensitivity data, we used a model composed of three detection mechanisms with the one most sensitive to any test wavelength determining observed threshold (*15*). The three mechanisms are (i) an opponent R/G mechanism, which detects most wavelengths longer than 500 nm and accounts for both peaks in that region; (ii) a "blue" (B) mechanism, which detects wavelengths shorter than 500 nm and is modeled simply by $P_{440}(\lambda)$ alone; and (iii) a "luminance" (L) mechanism, which detects the low-frequency test only at those wavelengths near the red-green crossover point where the response of the R/G channel is too small to permit detection by that mechanism. The spectral sensitivity of the L mechanism is taken to be V_λ, the standard photopic luminosity function. The spectral sensitivity of the R/G mechanism is taken to be proportional to the difference: $|P_{540}(\lambda) - kP_{570}(\lambda)|$. The constant k determines the spectral red-green crossover point. Fitting curves A through C in Fig. 1 produced estimated crossover points within 2 nm of the respective background wavelengths, thus capturing the effect of sliding the sensitivity trough to the wavelength of the background (*16*). The model's fit shows that this simple scheme does indeed account for the data in detail (*17*). Previous models of similar data (*5, 6*) have proposed two separate R/G opponent mechanisms, one responsible for the green peak and one for the red peak. The present, single

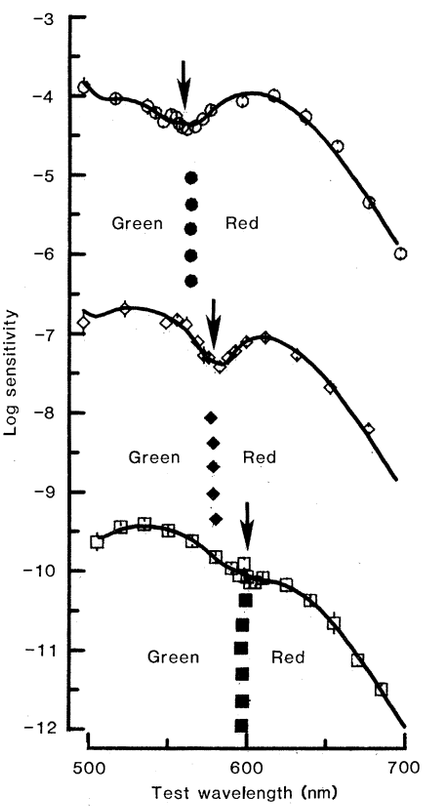

Fig. 3. Open symbols: low-frequency spectral sensitivity on adapting fields of 560, 580, and 600 nm (arrows) all at intensity $10^{9.0}$ quanta sec^{-1} deg^{-2}. Closed symbols: locus of unique yellow on the same backgrounds found with a wavelength staircase in which, at each intensity level, successive presentations of stimuli differing in wavelength were judged as either "reddish" or "greenish" (*4*). Observers: A.B. (560 and 580 nm) and B.S. (600 nm).

opponent R/G model is more parsimonious, and naturally links both threshold and suprathreshold observations.

JAY E. THORNTON
EDWARD N. PUGH, JR.
Department of Psychology, University of Pennsylvania, Philadelphia 19104

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14. This finding agrees with the results of P. E. King-Smith and K. Kranda [*ibid.* **21**, 565 (1981)].
15. See similar models by M. Ikeda [in (*7*)], S. L. Guth and H. R. Lodge [*ibid.* **63**, 450 (1973)], and C. R. Ingling and B. H. Tsou [*Vision Res.* **17**, 1075 (1977)].
16. Such a sliding would be expected from the model suggested by C. F. Stromeyer and C. E. Sternheim [*Vision Res.* **21**, 397 (1981)].
17. Fitting the model amounted to vertically translating the log sensitivities of the three mechanisms individually to minimize the squared deviation (summed over wavelength) between predicted and observed log sensitivity. For the R/G mechanism the crossover point was varied and then the red and green peaks were independently shifted vertically. Because of the isolation afforded by the low-frequency test, parameter estimates of the R/G mechanism were very robust. In particular, they were independent of assumptions about probability summation between the R/G and L mechanisms at the bottom of the sensitivity trough. We modeled probability summation by a power sum with an exponent of 4.0 [R. F. Quick, *Kybernetik* **16**, 65 (1974); (*6*)]. Below 500 nm, nonvisual pigments in the eye absorb strongly and alter the spectral sensitivity considerably from person to person; again the R/G parameter estimates were unaffected.
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Synchronized Moulting Controlled by Communication in Group-Living Collembola

Abstract. *Group-living Collembola of the genus* Hypogastrura *coordinate their moulting by communication. Animals of different ages and moulting rhythms synchronized the moulting rhythms when combined in a single culture. This synchronization is apparently not dependent on external stimuli but is coordinated by chemical communication among these insects.*

In insects, moulting is commonly synchronized by external stimuli (*1*). Usually a stimulus applies only to one moult, such as when the diapause of a specific instar is terminated by a phenological cue. In group-living species of the collembolan genus *Hypogastrura*, I found that moults are synchronized within aggregates, each of which may contain hundreds of thousands of animals (*2*). Apparently moulting is coordinated by chemical communication and is independent of the animal's age.

Experiments were carried out with *Hypogastrura lapponica* and *H. socialis*, which were kept in chambers (3.5 cm in diameter and 3 cm high). A moist bottom layer of plaster of Paris and sand ensured favorable humidity in the cultures. Small pieces of bark covered with algae (*Pleurococcus*), which were replaced about once a week, served as food and shelter, and the animals usually moulted under them. The cultures were inspected every day, and if any animal had moulted since the previous inspection, the whole 24-hour period was included in the moulting interval of the culture.

The importance of communication between animals was tested in two ways: by splitting a synchronized mother culture and by combining animals from different mother cultures with different moulting rhythms. Each mother culture consisted of animals of the same age. In tests with combined cultures, the animals were chosen so that their size (age) differences were sufficient to allow them to be distinguished after mixing. Cultures to be compared were exposed to the same physical conditions in a climate room.

Figure 1 shows synchronized moulting of an undisturbed culture of *H. lapponica* at 10°C. Three stages of the moulting cycle—premoult, moult, and postmoult—were observed. During the premoult period, the animals are inactive and tightly aggregated, and the distal part of their legs and antennae become white as the old cuticle detaches from the new one. This stage lasts 2 to 3 days in each animal before moulting is completed. During the postmoult period (usually about a week) the animals feed or are active in other ways. Variations in temperature or light did not affect the synchrony of moulting.

A synchronized mother culture of *H. lapponica* was divided immediately after all members had completed their first moult and many, but not all, had started to feed on the bark algae. By further separating the feeding animals from those that had not yet started to feed, two cultures which, on the average, had completed the last moult at slightly different times, were obtained. If the feeding animals had not been separated from those not yet feeding, they would all presumably have continued to moult synchronously. After the separation, the two groups soon went out of phase (Fig. 1B).

New cultures were started by combining animals from several mother cultures. All individuals in the daughter cultures synchronized their moulting shortly after mixing. During the synchronization process, the postmoult period became prolonged in some daughter groups and shortened in others, but the duration of the premoult and moult periods was not altered (Fig. 2).

The moulting cycle appeared to be-

Table 1. Moult synchronization in *Hypogastrura lapponica* and *H. socialis* tested by combining groups that originally moulted at different times. Abbreviation: LD, light-dark cycle (hours).

Groups combined (*N*)	Animals per group (*N*)	Light regime	Temperature (°C)	Moult at synchronization
		Hypogastrura lapponica		
4	5	(LD, 17:7)	10	2
3	3	(LD, 17:7)	10	4–5*
3	7	(LD, 12:12)	10	3
2	7	Dark	15	2
		Hypogastrura socialis		
2	30 + 10	Light	15	2

*Before synchronization, about 50 animals hatched from eggs laid at the beginning of the experiment.