Color Vision #2

Neural representations of color.

Deficiencies in color vision.

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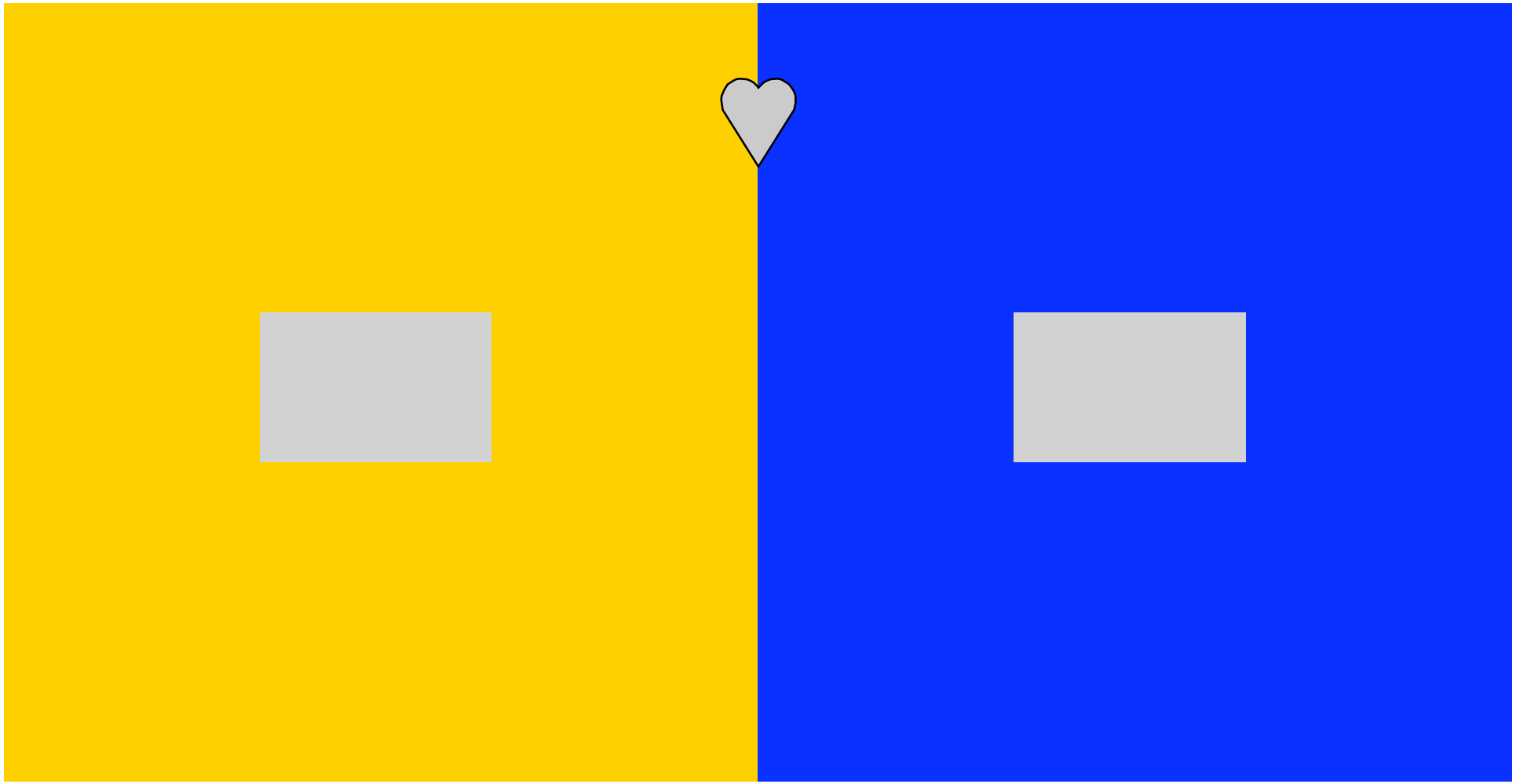
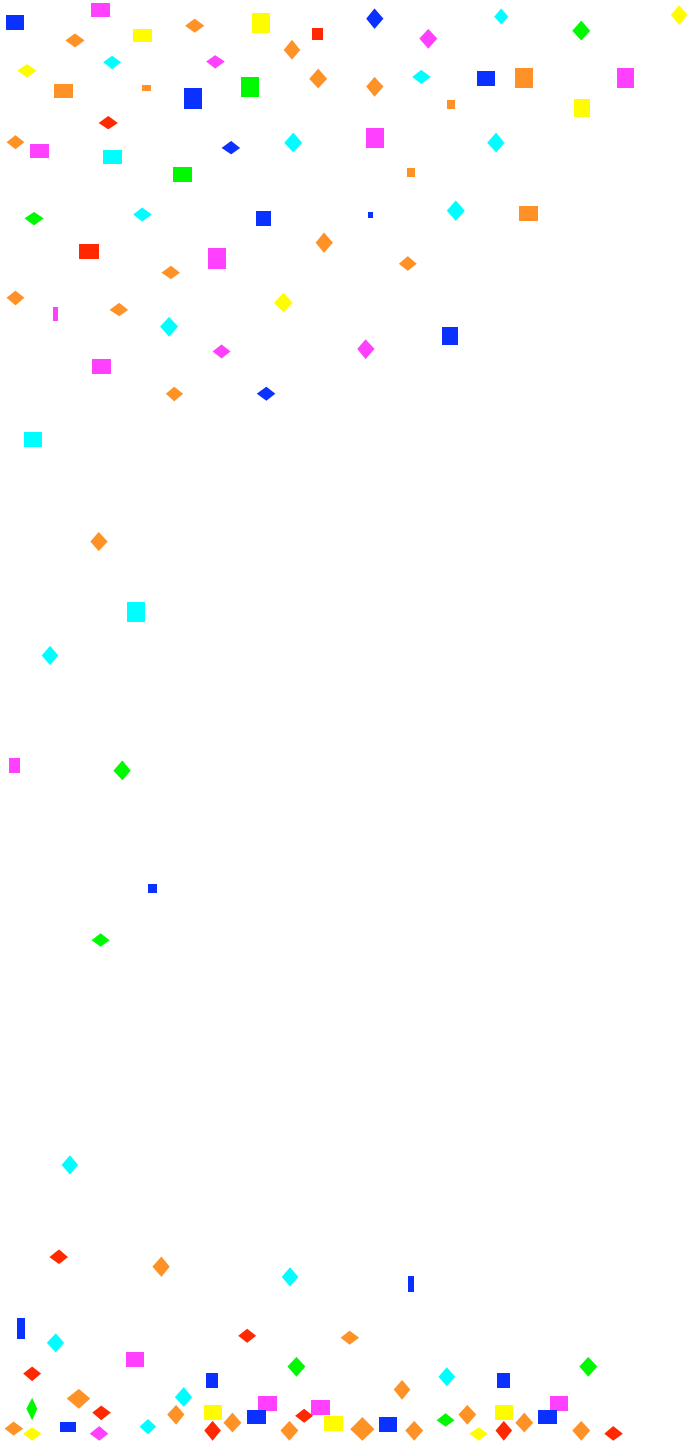
Nagging challenges (pre-1960) to trichromatic theory, which suggested to many that color vision derives from "opponent processes" (Hering, 1878).

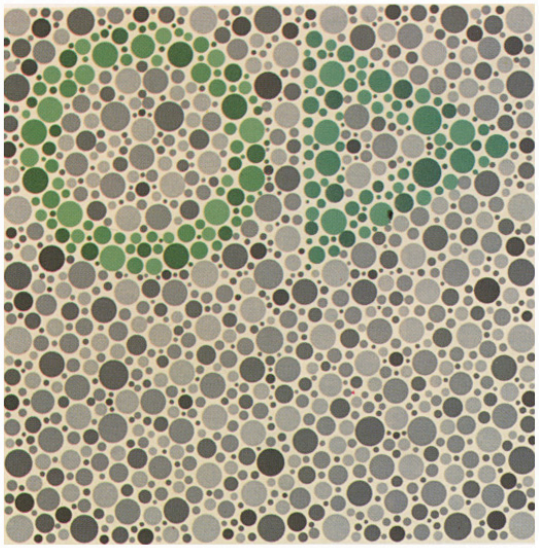
- **Subjective uniqueness of yellow**: Most people agree that yellow appears subjectively different from either red, green, or blue, and just as "primary". When subjects try to name colors rapidly, these 4 categories are more rapidly and more reliably named than others. This also occurs cross-culturally, not dependent on color names in particular languages.
- **Negative afterimages**: Why should prolonged exposure to blue (yellow) light produce a yellow (blue) afterimage? For that matter, why should red and green each produce an afterimage of the other unless they are somehow opposed to one another? Is the explanation that colors are encoded by opponent processes—R v. G, and B v. Y?
- **Simultaneous color contrast**: If a white or gray patch is surrounded by a larger area of intense color, the "opponent" color is seen in the neutral area. This also includes "brightness contrast", involving *contrasts* between shades of black and white.
- **Color blindness**: Why do color blindness and anomalies produce deficiencies in discriminating between pairs of colors—R v. G and B v. Y?
- **Sensitivity of color discriminations**: Another possibly related puzzle is how such similar and broadly tuned filters (as given by cone absorption spectra) can yield such exquisitely precise color discriminations—with wavelength discriminations ~1 nm, and 100s of thousands of visually different colors.

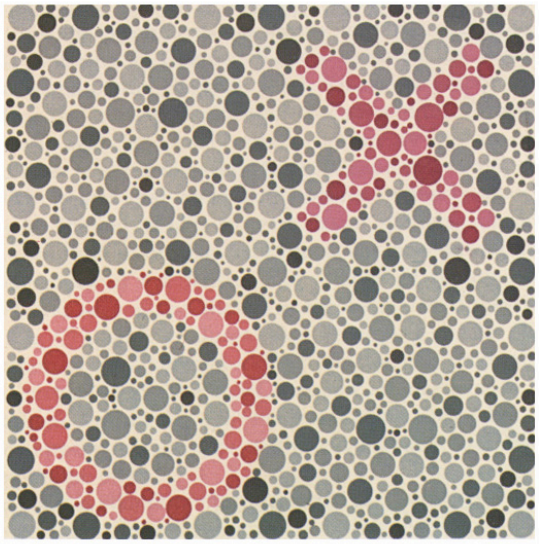
Afterimages and contrast effects

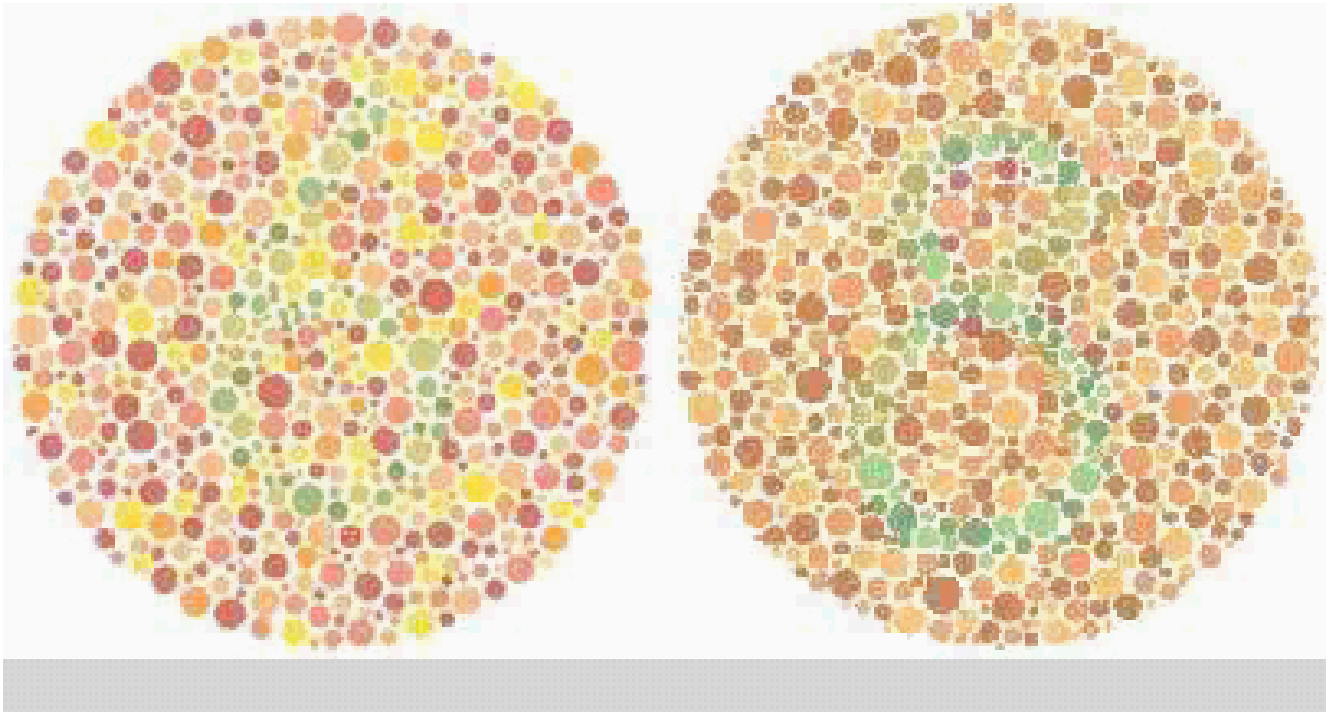




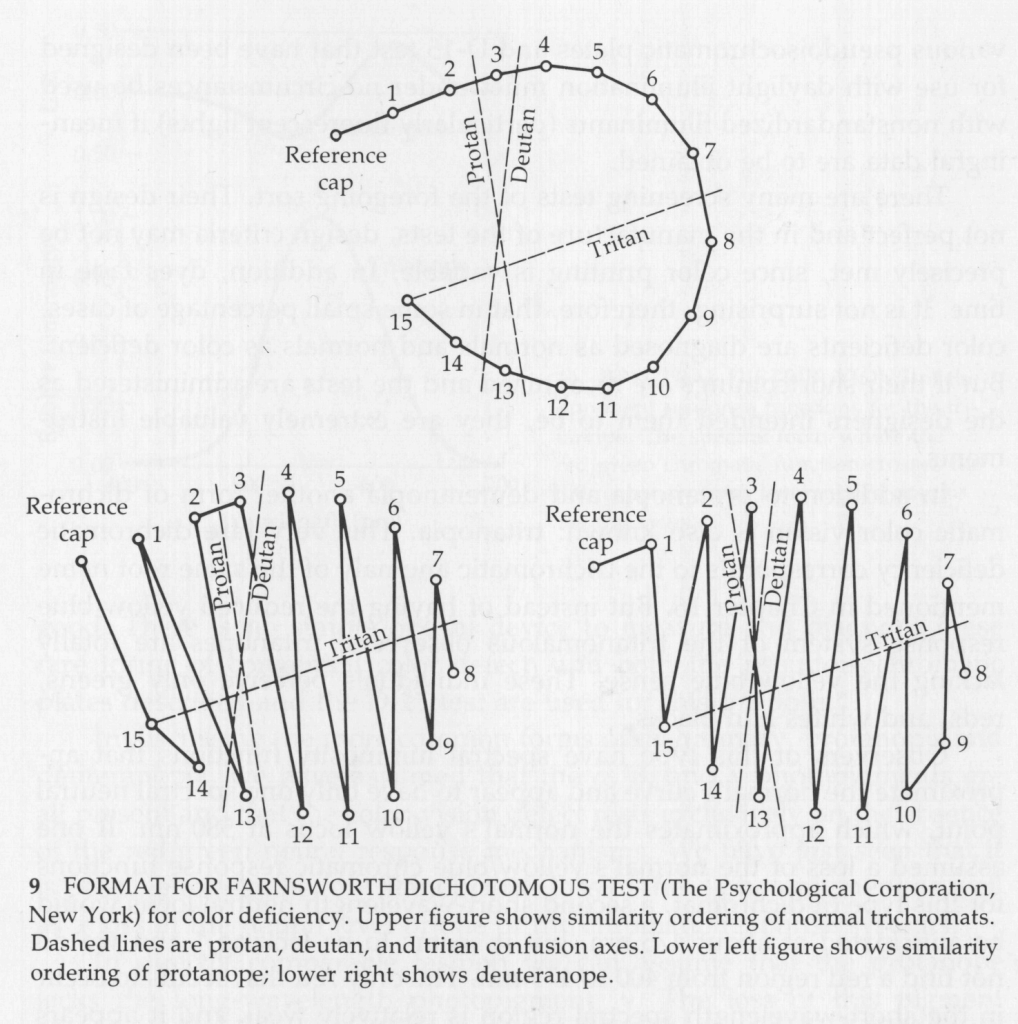
The Hardy-Rand-Ritler and Ishihara Tests for R/G Color Deficiencies





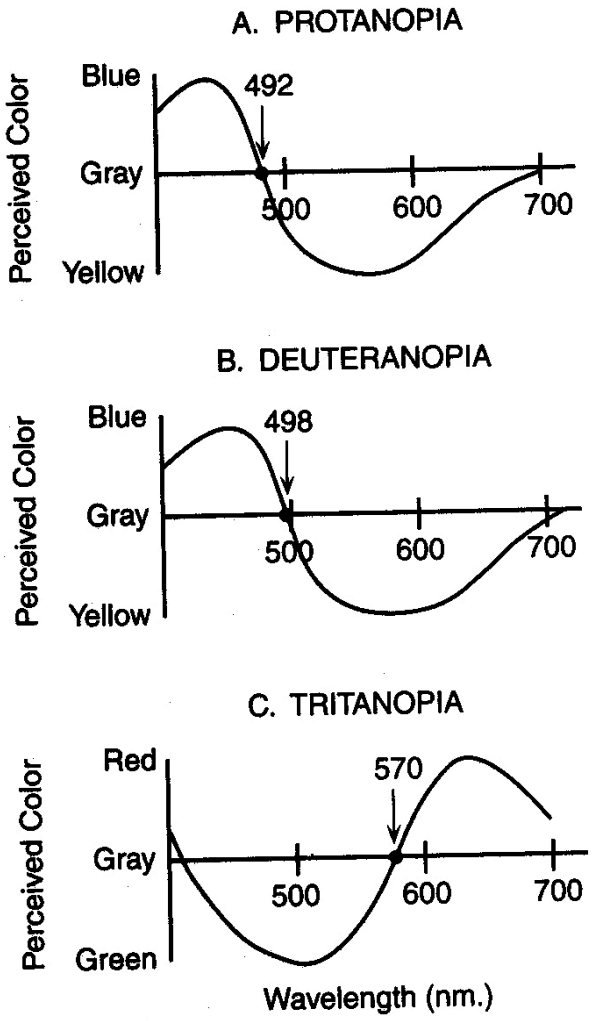


The Munsell-Farnsworth Tests



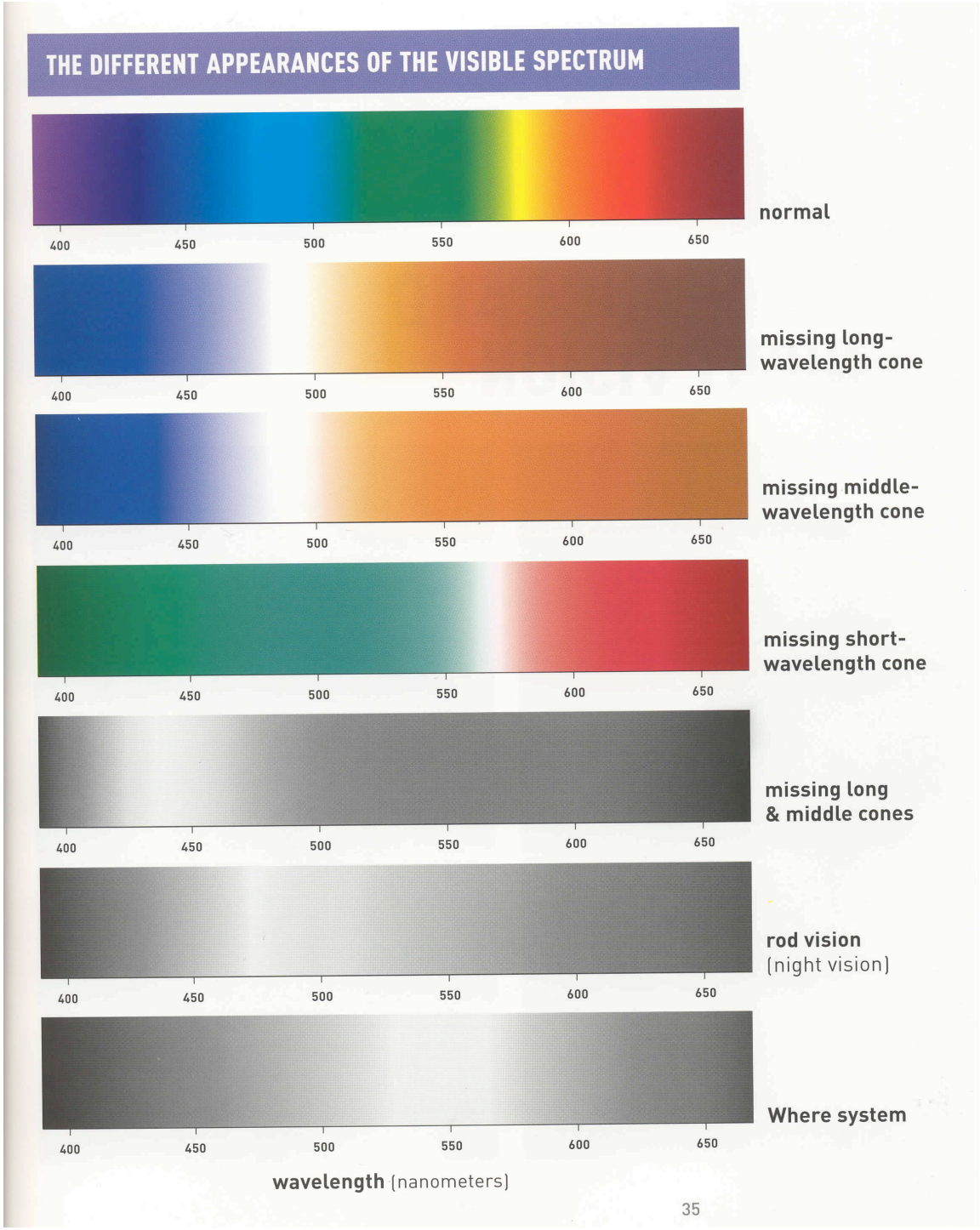
9 FORMAT FOR FARNSWORTH DICHOTOMOUS TEST (The Psychological Corporation, New York) for color deficiency. Upper figure shows similarity ordering of normal trichromats. Dashed lines are protan, deutan, and tritan confusion axes. Lower left figure shows similarity ordering of protanope; lower right shows deuteranope.

Neutral point tests for dichromacy



The illustration at the right is taken from M. Livingstone (2002), *Vision and art: The biology of seeing*, p. 35. New York: Harry Abrams.

Can you explain why the 2nd & 3rd panels are so similar? Why do the 2nd, 3rd, & 4th panels contain a bright white region not in the top panel? Why are the bottom 3 panels achromatic?



How Russell De Valois & colleagues resolved the issue of trichromatic vs. opponent-process theories:

De Valois (1965) and De Valois, Abramov, & Jacobs (1966) discovered how color information is encoded in retinal ganglion cells (recorded in LGN). They found that both theories were correct, each about a different stage of the neural process.

First, spectral sensitivities and color discriminations of several species of monkeys were determined by behavioral testing. (See diagram.) An old-world species (macaques) exhibited color discriminations essentially like those of humans with normal color vision; but some new-world species (e.g.,squirrel monkey) exhibited anomalous trichromacy similar to that of a protanomalous (red deficient) human. One of the tests was the *neutral point test* — which macaques passed with ease, but caused great difficulty for squirrel monkeys. Squirrel monkeys had difficulty with the neutral point discriminations near 480 nm. Another informative test was the *Rayleigh match*, which requires the subject (monkey or human) to discriminate between a monochromatic yellow and an additive mixture of red and green. Macaques and normal human observers fail to discriminate a wavelength of ~550 nm (Y) from an approximately equal mixture of 565 and 535 nm. Protanomalous humans and squirrel monkeys, however, require much more red than green for visual equality of the monochromatic yellow and the red+green mixture.

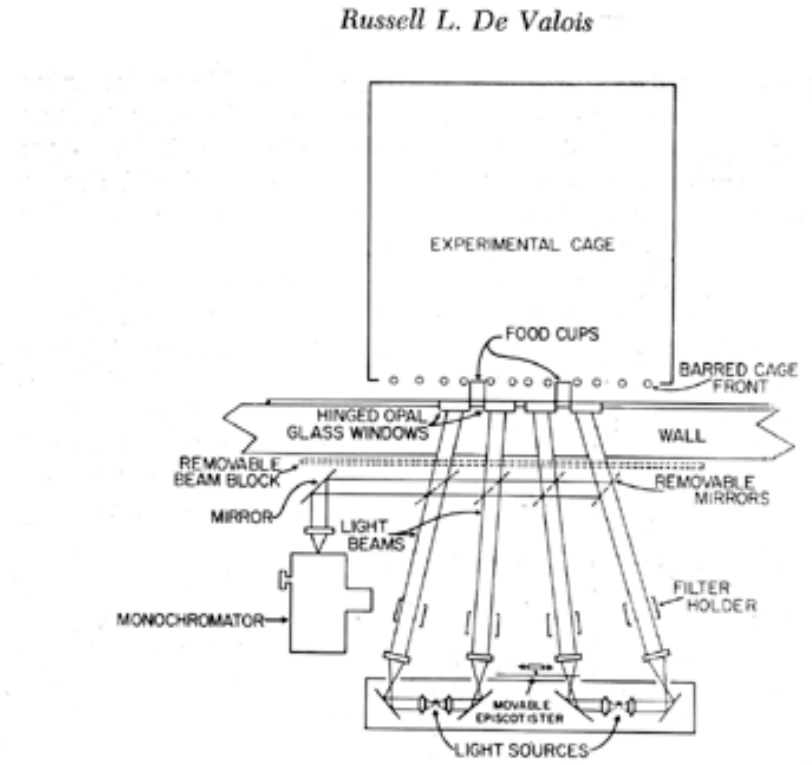


FIG. 1. Diagram of the apparatus used in behavioral testing of the visual sensitivity and color vision of monkeys.

Responses of LGN cells to varying wavelengths found by De Valois, Abramov, & Jacobs (1966) — spectrally opponent cells

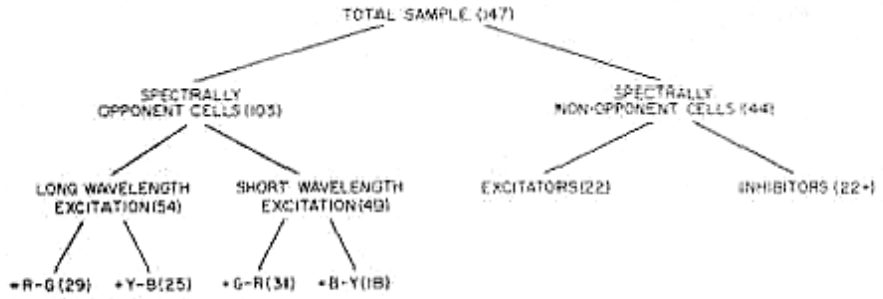


FIG. 3. Classification of the cells in the sample reported here. Numbers in parentheses refer to the number of cells in each category.

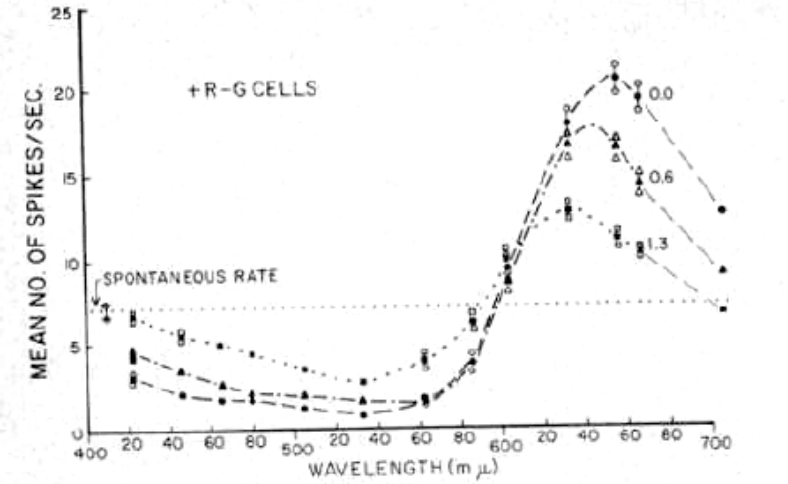


FIG. 9. Mean response curves for +R−G cells to an equal-energy spectrum. Numbers next to each curve represent log attenuation relative to maximum available. Open symbols and vertical lines at each point enclose one standard error of the mean. Dotted horizontal line gives, for this type, the mean firing rate in the absence of stimulation.

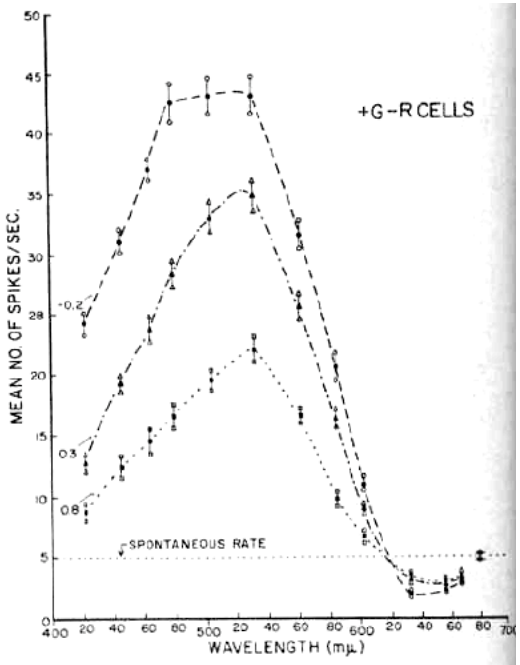


FIG. 11. Mean spectral response curves for +G−R cells. Details as for Fig. 9.

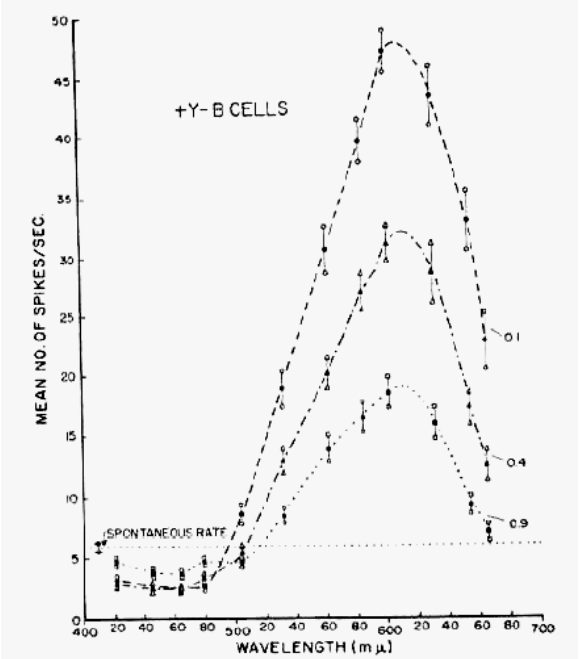


FIG. 10. Mean spectral response curves for +Y−B cells. Details as for Fig. 9.

Spectrally opponent cells carry color information;
non-opponent cells carry brightness information.

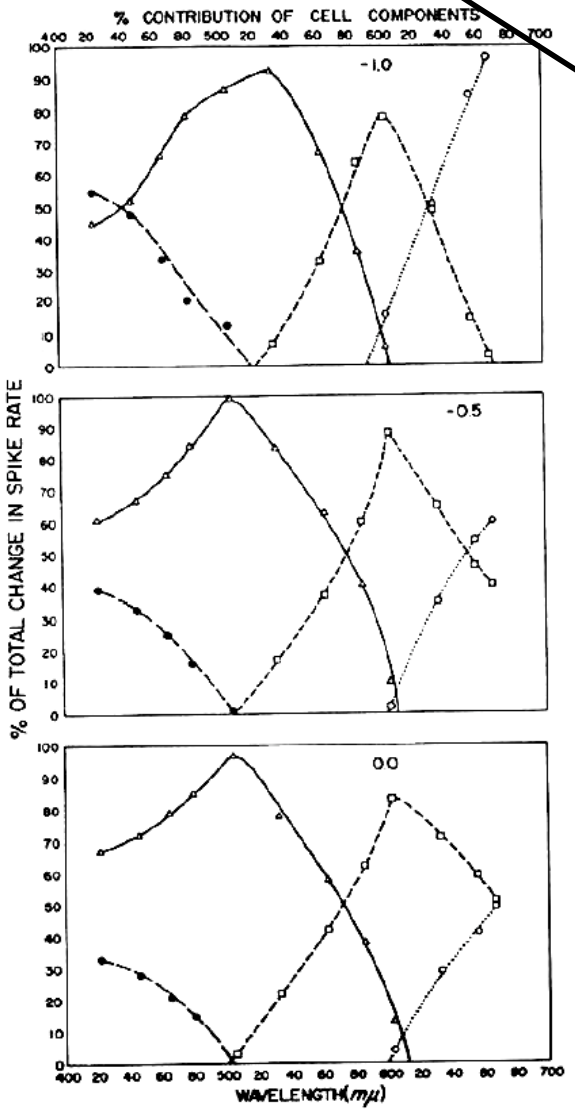


FIG. 21. Contributions, at three luminances half a log unit apart, the top graph being the lowest, of each of the four components underlying the responses of the opponent cells. (○·····○) +R and −R, (□– – –□) +Y and −Y; (△– △) +G and −G, (●— —●) +B and −B. See text for derivation of the components and method of computation.

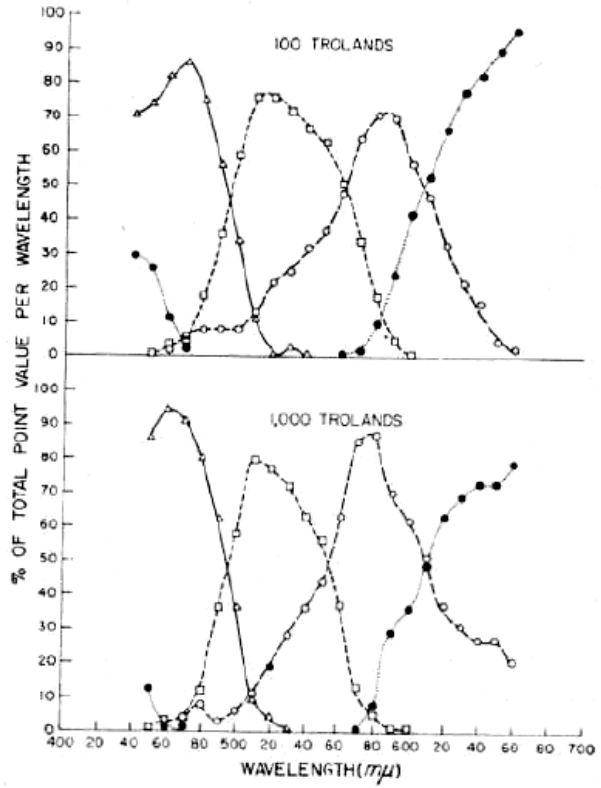


FIG. 20. Color naming as a function of wavelength. (△—△) blue, (□– – –□) green, (○— —○) yellow, (●·····●) red. Replotted after Boynton and Gordon.[10] See text.

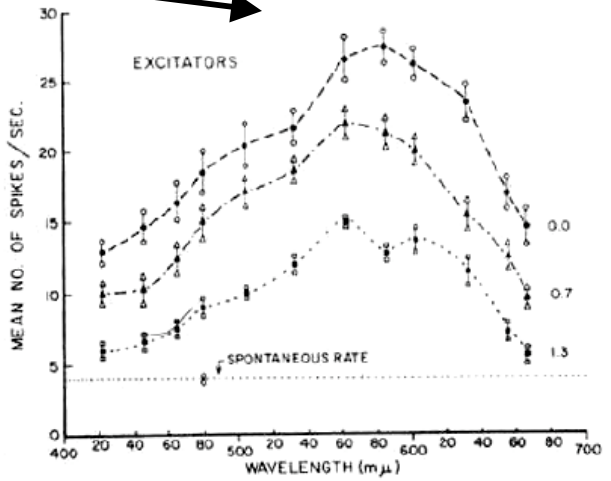


FIG. 16. Mean spectral response curves for nonopponent excitatory cells. Details as for Fig. 9.

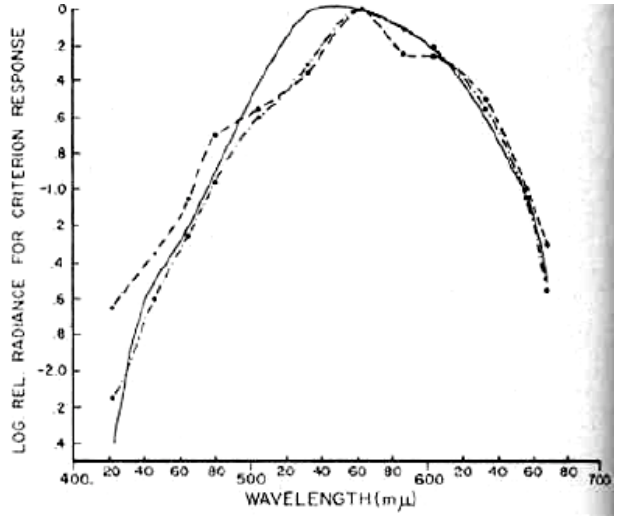


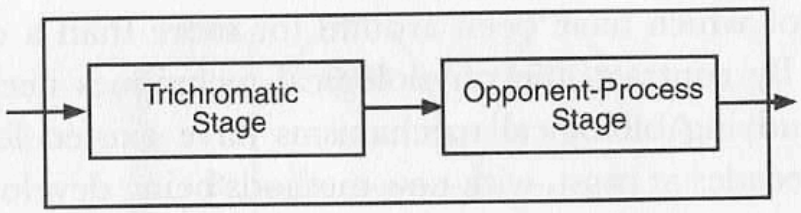
FIG. 17. Equal-response spectral sensitivity functions (respon criteria: (●— —●) 14 spikes/sec, (●— ·—●) 18 for nonopponent e citatory cells compared with the CIE photopic luminosity functi (—).

De Valois and opponent processing of color in LGN

De Valois et al. found three main categories of retinal ganglion and LGN cells: Two of these were color-opponent and another was "broad-band" or non-opponent. The color-opponent cells gave excitatory responses to some wavelengths and inhibitory responses (reductions in firing rate) to other wavelengths. Most of these cells were red-green opponent, excitatory to red and inhibitory to green, or vice versa. A smaller number were blue-yellow opponent cells, excitatory to blue light and inhibitory to yellow, or vice versa. Color adaptation tests (where the monkey's eye was flooded with red light, for example) demonstrated that the blue/yellow opponent cells receive inputs from both L- and M-cones, with the same sign from both (either excitatory or inhibitory). Many of the cells were found to be non-opponent, giving the same response (excitatory or inhibitory) to lights of all wavelengths. Evidently, these cells signal achromatic information about brightness.

Text-book diagrams of the arrangement are shown below.

Spatial relations involved in these color mechanisms are not shown in these diagrams, but this spatial aspect is very important. Color opponency is combined with spatial opponency — providing information about spatial derivatives of color.



DUAL PROCESS THEORY

Figure 3.2.12 Hurvich and Jameson's dual process theory of color vision. An initial trichromatic stage (à la Helmholtz) provides the input for a second opponent process stage (à la Hering).

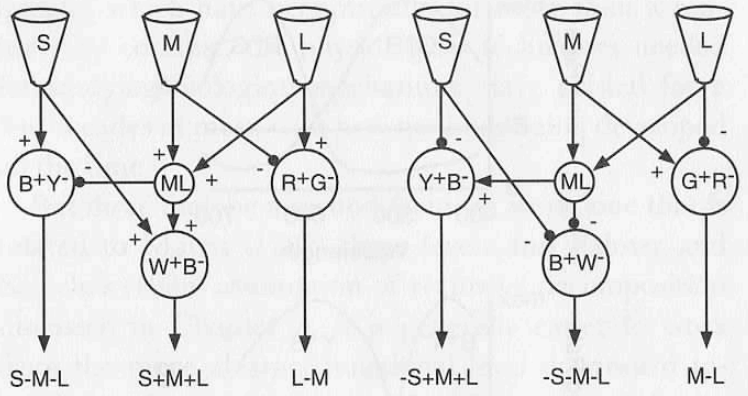
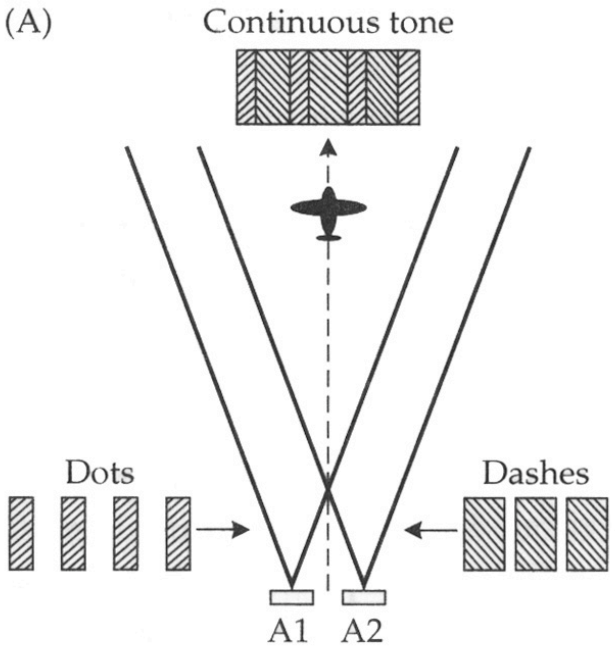


Figure 3.2.15 Possible neural circuits for dual process theory. Opponent responses are derived from S, M, and L cone outputs by excitatory connections (arrows) and inhibitory connections (solid dots). The ML units encode the sum of activities in the M and L cones.

Opponent processing is a general method for dramatically increasing signal resolution.

David Regan (2000) describes a method used to guide Luftwaffe bombers that defied British understanding in WWII The method was not understood by British intelligence nor by Nobel laureate P.M.S. Blackett, but Regan suggests that it could have been readily understood by a student of vision familiar with opponent processing of color signals.

The method of opponent processing of outputs from initial filters seems to be used throughout the visual system — for contrast (e.g., center-surround organization of ganglion cell receptive fields), orientation sensitivity, spatial acuity, motion, and other aspects of spatial vision. In color vision, this mechanism offers the best explanation for how visual discriminations of many millions of colors are obtained from the outputs of just 3 broadly tuned filters.



Summary & conclusions:

- Several characteristics of color vision suggest that colors are encoded by "opponent processes".
- Color deficiencies, for example, produce poor discriminations between *pairs* of colors — R v. G or B v. Y.
- The resolution of the long-standing discrepancies between these two alternative theories was resolved by the neurophysiological research of De Valois and colleagues in the mid-60s.
- Opponent-processing is a general and powerful method for increasing signal resolution, and is widely used in the visual system.
- Much is now known about the genetics of color deficiencies in color vision. The main variations seem to be related to the cone pigments themselves rather than the relative numbers of cones.