

## TENSORIAL APPROACH TO COLOR VISION

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### Abstract

Color vision is approached on the basis of tensor network theory. The model unifies the psychophysical with the physiological and anatomical description. Lateral interactions in the retina provide an overall metric geometry for the generation of color signals by the retina via a covariant to contravariant transformation in the retinal network space.

### 1. Introduction

The problem of color vision has presented to both physiologists and physicists an enormous challenge since color vision is a secondary quality (Locke, 1690; Schroedinger, 1920; Smart, 1959). Indeed, color is 'created' by the brain from a continuous range of the electromagnetic frequencies known to us as light. Color represents, therefore, a functional property of the retina and of the central nervous system. This property is brought about by the opposing activity of specialized retinal photoreceptors which respond to particular light frequency ranges. Electrophysiological studies of receptor opposition (Naka and Rushton, 1966a,b; Werblin and Dowling, 1969; Fuortes and Simon, 1974; De Monasterio, Gouras and Tolhurst, 1975; Baylor and Fettiplace, 1977a,b; Burkhardt and Hassin, 1978; Piccolino, Neyton and Gerschenfeld, 1980) indicate that excitatory and inhibitory synaptic interactions in the retinal network encode the patterns of activity of the specific receptors. These patterns of neuronal activity are interpreted as color by the central nervous system.

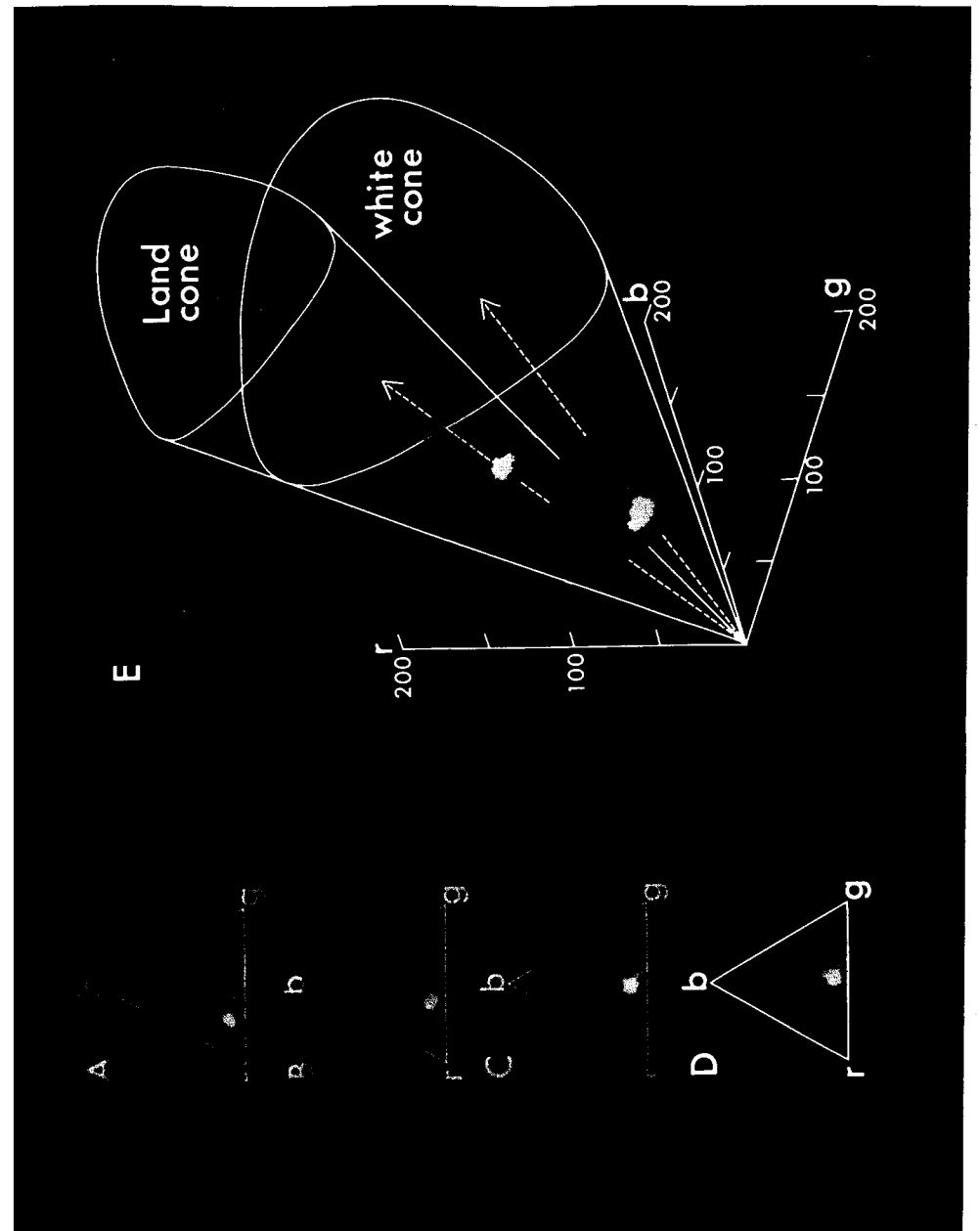
Color vision is actually generated by the interactions between neurons and is not necessarily related to particular frequencies of the electromagnetic light spectrum. This effect was demonstrated psychophysically in an epoch-making study by Land: he discovered that a complete range of color may be generated by particular mixtures of white and pink light (Land, 1959). Figure 1 A-D shows the change in color perception with change in background illumination and Figure 1 E shows the complete spectrum generated by a restricted ambient light range. The present paper, in addition to giving a model for the acquisition of color from a continuous spectrum, offers a formal explanation for the Land phenomenon.

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**Fig. 2.** Wiring diagram of the generalized vertebrate retina (modified from Siminoff, 1980). Cell types are relabelled to simplify notation. *r*: red receptor; *g*: green receptor; *b*: blue receptor; *s*: surround; *c*: center; *arrow*: depolarizing input (for *D* bipolar cell, hyperpolarizing); *circle*: hyperpolarizing input (for *D* bipolar cell, depolarizing); *L*: local horizontal cell, *A, B, C, D*: horizontal cells; (-) hyperpolarization; (+) depolarization; *a, β, γ, δ, ε, ζ, η, θ*: bipolar cells; *H* on a bipolar cell: hyperpolarizing; *D* on a bipolar cell: depolarizing. Colored stripes on receptor and horizontal cells approximate the color of the frequency of peak sensitivity of the receptor or receptor contri-

O'Bryan, 1971; Fuortes and Simon, 1974; Normann and Pochobradsky, 1976; Pasino and Marchiafava, 1976; Burkhardt, 1977), the multi-receptor response and center-surround organization of each bipolar cell (Werblin and Dowling, 1969; Kaneko, 1973; 1977; Schwartz, 1974; Richter and Simon, 1975; Naka, 1977), and the pairing by color of hyperpolarizing and depolarizing bipolar cells (Werblin and Dowling, 1969; Daw, 1973; Kaneko, 1973; Schwartz, 1974; Richter and Simon, 1975). The tensor transformation summarizing all these effects is the transformation from receptor to bipolar space.

The transformation can be worked out term by term: Let the transfer function from neuron  $X$  to Neuron  $Y$  be  $Y^X$ , so that the polarization  $x$  of neuron  $X$  is transformed into the summand  $Y^X(x)$  of the polarization of neuron  $Y$ . The sum approximation to neuronal integration is reasonable for the retina (Siminoff, 1980).

The superscripts  $c$  and  $s$  stand for center and surround. They are not at present being used as tensor indices. In writing the transformation, separate out the actions of  $L^s$  and  $L^c$  on the receptor cells. Assume that they perform the same set of transfer functions, on the grounds that every local horizontal cell  $L$  is central to some bipolar cell. Then the action of the  $L$ -cell on the receptor space vector  $P_n = (r, g, b)$  is given by

$$M_j^n = \begin{bmatrix} 1 + r^L L^r & r^L L^g & r^L L^b \\ g^L L^r & 1 + g^L L^g & g^L L^b \\ b^L L^r & b^L L^g & 1 + b^L L^b \end{bmatrix}$$

This expresses the summation by the  $L$ -cell of the polarization of each receptor and their inhibition as a function of that polarization. The original polarization of the receptors is carried through by the terms of the diagonal.

The whole transformation from receptor polarization vector  $P_n$  to bipolar polarization vector  $B^b$  is given by

$$B^b = D^{bj} M_j^n P_n^{(c)} + H^{bj} M_j^n P_n^{(s)}$$

where  $D^{bj}$  acts on center receptors and  $H^{bj}$  expresses the effects of surround receptors as mediated by the horizontal cells. Then

$$H^{bj} = \begin{bmatrix} \alpha^A(A^{L^s}L^{sr^s} + A^{r^s}) & \alpha^A A^{L^s}L^{sg^s} & \alpha^A A^{L^s}L^{sb^s} \\ \beta^A(A^{L^s}L^{sr^s} + A^{r^s}) & \beta^A A^{L^s}L^{sg^s} & \beta^A A^{L^s}L^{sb^s} \\ \gamma^B B^{L^s}L^{sr^s} & \gamma^B(B^{L^s}L^{sg^s} + B^{g^s}) & \gamma^B B^{L^s}L^{sb^s} \\ \delta^B B^{L^s}L^{sr^s} & \delta^B(B^{L^s}L^{sg^s} + B^{g^s}) & \delta^B B^{L^s}L^{sb^s} \\ \varepsilon^C(C^{L^s}L^{sr^s} + C^{r^s}) & \varepsilon^C(C^{L^s}L^{sg^s} + C^{g^s}) & \varepsilon^C C^{L^s}L^{sb^s} \\ \zeta^C(C^{L^s}L^{sr^s} + C^{r^s}) & \zeta^C(C^{L^s}L^{sg^s} + C^{g^s}) & \zeta^C C^{L^s}L^{sb^s} \\ \eta^D D^{L^s}L^{sr^s} & \eta^D D^{L^s}L^{sg^s} & \eta^D(D^{L^s}L^{sb^s} + D^{b^s}) \\ \theta^D D^{L^s}L^{sr^s} & \theta^D D^{L^s}L^{sg^s} & \theta^D(D^{L^s}L^{sb^s} + D^{b^s}) \end{bmatrix}$$

and

$$D^{bj} = \begin{bmatrix} \alpha^{r^c} & 0 & 0 \\ \beta^{r^c} & 0 & 0 \\ 0 & \gamma^{g^c} & 0 \\ 0 & \delta^{g^c} & 0 \\ \varepsilon^{r^c} & \varepsilon^{g^c} & 0 \\ \zeta^{r^c} & \zeta^{g^c} & 0 \\ 0 & 0 & \eta^{b^c} \\ 0 & 0 & \theta^{b^c} \end{bmatrix}$$

Consideration of these matrices confirms the intuitive observation that off-center receptors combine, via the horizontal cells, with center receptors to give complementary pairs of bipolar cells. Each depolarizing bipolar cell is paired with a hyperpolarizing bipolar cell of the same color or set of receptor inputs, but of opposite sign. Each bipolar cell has a center-surround organization, such that a color input from surrounding receptors will be subtracted from that same color from receptors central to the bipolar cell. Thus, the bipolar cell activity is related to differences of receptor responses; all together, the bipolar vector is a difference vector found by subtracting vectors in receptor space.

That is, the visual system is responding to difference vectors, which retain sufficient variation to give the entire spectrum, rather than to the absolute polarization vectors, which are restricted in polarization space. At any instant, the sets of bipolar pairs establish local coordinate systems of difference vectors varying over the retina. Figure 1 A–D is an expression of this variation: the same receptor polarizations are transformed into different colors depending on the background, that is, on the local coordinate system.

It must be emphasized that the precise organization of the retinal elements is not a central point in our model. The important consideration is that a particular class of geometrical transformation be implemented. The Siminoff generalized retinal network is only one of an enormous class of possible neuronal networks capable of generating this transformation. In fact, it is quite possible that the actual details of implementation may be different in different species, even in such apparently important aspects as the precise connectivity of the retinal network.

### 3. Tensorial interpretation of the Land phenomenon

This scheme provides a coherent model of color vision applicable even to complex cases such as the Land phenomenon (Land, 1959). In the Land phenomenon, all colors are seen even though the illumination is only red and white. Figure 1 E shows the change in the color cone when the light is restricted to mixtures of red and white. Receptor excitations that are seen as white in white light are seen as green in red light. This can be demonstrated by illuminating a room with one white and one red lamp and casting a shadow of the red lamp: the shadow appears green. Similarly, receptor polarizations that are interpreted as red in white light become white in red light.

In these cases with red background, each local set of covariant components of the receptor vector determined by the local background adapts by changing the way in which red is measured: A vector which in white light points into the red is rotated in a red background by the shortening of the red components. Thus, the receptor can be seen, after the transformation by the metric, as green, blue, or any other color.

While receptor cells are discrete, they are joined by a lateral network that unites them into a single color field. All together, the local neuronal networks form a single metric tensor. The proposal that color vision functions according to a metric tensor expresses the idea that the color field, instead of being an aggregate of separate points, is coherent across the retina.

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