XXI. NEUROPHYSIOLOGY[*]

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A. COLOR VISION I

The range of visible light lies between 4000 Å and 7000 Å wavelength. Extremely powerful radiation above and below those limits can be seen, but these are the commonly accepted extrema. Within that band the spectral distribution of power in a ray of light describes some of its qualities. The color that is perceived seems to be related to that spectral distribution. Two of the operations that one can imagine to be made on the distribution are

1. Integration of power along the spectrum weighted by a function of position in the spectrum; and

2. A description of the distribution of power that is normalized with respect to total power, that is, the power in every region of the band divided by the power in the whole band.

The first operation takes (a) the "intensity" of light, and the second gives us the "quality." A suitable handling of the quality can be made to show (b) where power is greater along the spectrum, and (c) how much greater it is there than elsewhere. Our subjective impression for a uniform patch of light is that we see a color that has (a) brightness, (b) hue, and (c) saturation. These two triads of properties seem to be related.

Color perception can be studied in two aspects: the "aperture mode," and the "object mode." What I name as the color of a uniformly lit surface of a particular absorption spectrum depends greatly upon what other colors bound that surface, are in its neighborhood or have just preceded it in time on that surface. These effects are not negligible. Simultaneous and successive contrasts are involved in colored afterimages, colored shadows, color constancy, and all of those other visual phenomena studied in the mid-nineteenth century. But this topic of color in the real world — the "object mode" — is not discussed here; in this report I concern myself solely with what is called the "aperture mode," which is exemplified by this supposition: Suppose that my whole field of vision is a uniformly and neutrally colored matte surface in which there is a circular hole approximately 10° in visual angle. Let me partition that hole

into two semicircles and color the light coming through one uniformly. What manipulations with light are needed to change the other semicircle in such a way that I see a whole circle of uniform color? This method removes, as far as possible, the relation of color to form by rendering constant everything except color. Under such conditions, and for people with normal color vision looking directly at the hole, all colors can be matched by a combination of at least three colors; that is, three colors are sufficient, even though they may not be "real."

There are several principles that must be recalled before we continue.

1. Colors add to make a color.

2. A color cannot be dissected uniquely into component colors, and many different mixtures of different colors can give the same color.

3. Any color mixture, no matter how it is composed, must have the same appearance as the mixture of a certain saturated color (spectrum color or purple) with white.

4. Colors that look alike produce a mixture that looks like them.

5. When one of two kinds of light which are mixed together changes continuously, the appearance of the mixture changes continuously also.

(I recommend Chapter 20 in Helmholtz's Physiological Optics for further study.)

6. The laws of color mixture can be expressed as a barycentric operation on the spectral colors. If you think of the spectrum laid out along a wire, and have the wire bent round into an open plane figure, and if the power in a certain colored light everywhere along the spectrum is imitated by proportionate weights attached to the wire, then the center of gravity of the figure represents the resultant hue and saturation, and the weight of the whole figure represent the intensity of the color.

These are Newton's laws of color, and they have not been modified since his time. Grassman formalized these laws after Newton. Helmholtz gives a beautiful exposition of how they are used. Maxwell brought them to their modern form. The experimental problem is to erect the correct shape of the spectrum boundary of this figure, and Helmholtz shows how this can be done. The spectrum is not closed on itself as Newton had it, but is open just as a bent hairpin, and the colors, represented by mixtures of the extrema of the spectrum (the purples), lie along a straight line between the spectral extremes.

Once this barycentric method has been conceived, it is clear that, since any closed plane figure can be enclosed in a triangle, the same operation can be performed by using only three colors, one at each vertex of the triangle, with the power at any point in the spectrum considered a resultant of powers concentrated at those three points. Thomas Young announced this notion in its physiological form — that three types of retinal cell, each sensitive to a different color, were enough to describe a color space. This was later elaborated by Helmholtz.

But while Newton's laws ensure that the color plane is everywhere not concave, it

is everywhere convex over the locus of spectral colors, and straight only over the purples. Thus, of the colors needed to describe the color figure completely, two must lie outside the color figure, that is, they are imaginary. And, indeed, the reference colors in colorimetry are of this sort.

We are now able to continue our discussion of matching colors seen through the 10° aperture. Since I must use real lights and colors, I find that if there is a test color in one-half of the aperture and the three mixing lights are noncolinear (that is, one of them cannot be matched by a mixture of the other two), then I can either match the test color by an appropriate unique mixture of the other three or I can add one of the three to the test color and match a unique combination of these two by a unique combination of the other two. There is no set of real colors which I can choose for which, over all of the saturated colors to be matched, no color must be switched to the test side (that is, the intensity of that component is negative). Using four colors rather than three is no advantage, incidentally, for, since the locus of spectral colors is everywhere convex, at least two of the colors used for matching still will have to be imaginary, that is, they will have negative intensities for some of the saturated colors to be matched. The same is true for however many saturated colors that could be used to made a match; some of them will have to take on negative values in matching some other saturated colors. There is no advantage, then, in using more than three colors in colorimetry, and it is not as if there were a set of errors in the trichromatic scheme, which can be completely corrected by the use of one more color judiciously chosen.

"Color" is used here both as the subjective perception of light and as the physical properties of the light. Miss Ladd-Franklin was very severe with Helmholtz for doing this. I shall assume that the reader distinguishes "color" as a description of the intensity and quality of light from "color" as a description solely of the quality (when the intensity is being varied, as in color matching), from "color" as a subjective point in psychophysical space having intensity, hue and saturation, from "color" as the percept of hue and saturation independent of brightness. These distinctions are clear in context, I believe.

Having looked at color matching in the aperture mode and finding a trichromatic scheme sufficient, we now ought to consider the physiological question. Young, who knew about the discrete character of the retina — that it was a mosaic — (after all, Descartes based his theory of vision on the fact that the optic nerve fibers were separate elements), felt that it was unlikely that each fiber should have infinite modes of resonance, or the capacity to display simultaneously that which a spectrophotometer must do in time. Accordingly, he proposed, in fact, that the retina has three sorts of elements: one sensitive to red, another to blue, and a third to green; and that with these three types uniformly distributed color vision could be explained. This idea was taken up enthusiastically by Helmholtz, and the physiological consequence is the three-receptor hypothesis fitting with a trichromatic scheme of color matching. Another

physiologist, Hering, who was much taken by the notion of complementary colors, as implied by the barycentric system of Newton and measured by the nineteenth century physiologists, carefully pointed out that, since red was the complement of green and blue of yellow (as Democritus had remarked two millenia earlier), a three-duet system actually occurs physiologically. That is to say that we see color by virtue of taking an opposing relation between how much a "red" process is affected versus how much a "green" process is affected, so too "blue" vs "yellow" and "black" vs "white". The claim is advanced that this scheme accounts better for the facts of color blindness. A great deal of tedious nonsense cloaks this controversy. None of the evidence distinguishes the Hering from the Helmholtz notion, for, in fact, they are the same. To understand why, we must go back to the notion of colorimetry. The center of gravity of a triangle ABC, where the weights a, b, and c are concentrated at the apices, and the sum of the weights is constant, can be determined simply from the moments:

$$\frac{a}{a + b + c} AX, \qquad \frac{b}{a + b + c} BX, \qquad \frac{c}{a + b + c} CX,$$

where AX, BX, and CX are distances from each of the vertices to the center of gravity. If I use a fixed triangle, for which I know the distance of A to B, B to C, and C to A, then I also need to know the sum of all weights and two of the weights to determine where the center of gravity lies. Thus, if I know $\frac{a}{a + b + c}$ and $\frac{b}{a + b + c}$, it is sufficient for me to compute the center of gravity of a fixed triangle under the conditions given (that is, I need only to hang a triangle from two vertices to find the center of gravity). In fact, this is how modern colorimetry is carried out. We have all of the coupling here that we need. For example, if c is kept constant and a increases, then b decreases, and conversely, and all of this could be displayed entirely simply by one of the terms. The trichromatic scheme, when translated into a trichromatic physiological process, implies two things: First, only two of the three possible channels are required to provide all of the information about the color plane; and second, each of the colors denoted by each of the two channels will appear to be see-sawing with or opposing its complement. Hering's hypothesis, in the best light, modifies the Helmholtz hypothesis in this way: It is true that three colors are needed to erect the color space, but only two channels (that is, hue and saturation normalized against brightness) of output are required to carry information about the color plane. Total brightness, however, requires another channel.

When I speak about channels I imply that the processing of color data must occur very early in the visual system. There are several reasons for supposing this. First, there is an enormous dynamic range in our vision, and the reliable dynamic range of firing nerve fibers is not impressive. Second, any transformation of a continous

measure through a set of coupled nonlinear oscillators is bound to be noisy and it would seem a bit silly of nature to arrange for a noisy transmission only to recover the required signal by some sort of correlation process later; particularly, if the required signal can be achieved by direct methods earlier. Third, physiological studies on the optic nerve show that some such processing already occurs in the retina. Only the last reason is perfectly valid.

Although originally I planned to expound my particular theory of how color vision can be explained by form-function relations in the retina, I have now decided that this is premature. Those notions led me to the construction of a device to imitate color vision — but, since it could have been built purely by the laws of colorimetry, it proves nothing about my hypothesis.

Notice that the formula for determining the center of gravity is quite the same as
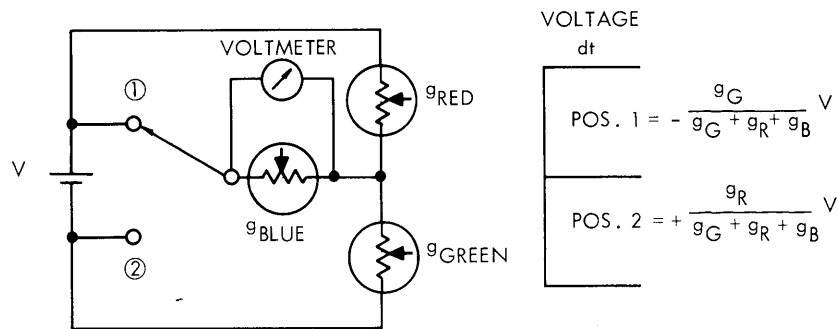
ALL PHOTORESISTORS SHOW LINEAR RELATION OF CONDUCTANCE TO THE POWER
OF AN INCIDENT LIGHT OF FIXED SPECTRAL COMPOSITION

g_{RED} = CONDUCTANCE OF PHOTORESISTOR OVERLAID WITH FILTER SO THAT CONDUCTANCE AS A FUNCTION OF WAVELENGTH FOR EQUAL ENERGY ILLUMINATION IS CURVE 1

g_{GREEN} = SAME AS CURVE 2
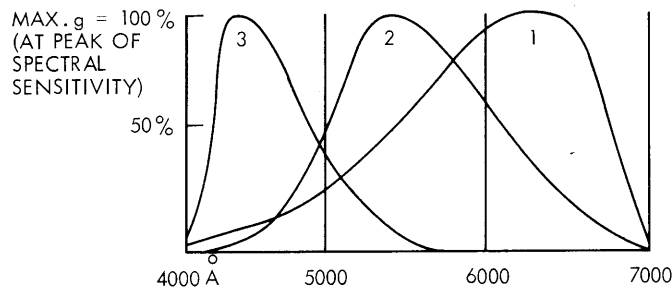
g_{BLUE} = SAME AS CURVE 3

Fig. XXI-1. The Maggie.

Kirchhoff's laws for determining voltage at the conjunction of resistors. For example, I assume photoresistors (PR) whose conductance is a linear function of the intensity of light playing on them, and which have a flat response in the visible band. That is, I can write the conductance of one filter-PR combination as a function of its spectral sensitivity, for example, g_R. If the switches are in the up position as shown in Fig. XXI-1 and all PR's have identical characteristics, then, if we call the amount of light passed by the red filter R, by the green, G, and by the blue, B, then E becomes

$$E_R = \frac{g_R}{g_R + g_B + g_G} V. \text{ If the switch is in the down position, } E = E_G = \frac{g_G}{g_R + g_B + g_G} V.$$

If E_R is taken to be the x-coordinate and E_G as the y, the locus of all "colors" that can be seen by this system lies within the triangle bounded by (0, 0) (0, V), and (V, 0). Furthermore, a particular spectral composition of light playing simultaneously on all three elements uniquely determines a point within this triangle, independently of the intensity of the light. This is a very simple system and is useful for explaining the Newtonian laws of color to students. They see very quickly how the " opponents" theory of Hering and the trichromatic theory of Helmholtz are identical, and the switch between g_R and g_B is useful to illustrate this likeness.

But to make a practical commercial device from this is a bit more difficult. For one thing, while there are several linear photoresistive materials, some of them have nasty troughs in the visible spectrum (for example, in Clairex No. 2 material), and others that seem smooth on the linear plot of sensitivity vs spectrum but are somewhat insensitive in the visible band turn out to be very irregular in their spectral response (for example, in Clairex No. 4). This is why I dislike using linear rather than logarithmic plots of sensitivity vs spectrum. In general, the Clairex No. 5 material is quite good, and, despite its irregularity in the yellow, is essentially of a monotonic fall-off from its peak at 5600 Å.

If the sensitivity of the material at each point P in the spectrum is S_p, then the problem is to devise a filter with the property that if it attenuates the power at P by a factor, Q_p, the response of the material covered by the filter, $Q_p S_p$, will give the wanted sensitivity characteristic over all p's.

In order to build a usable color space, I do not believe that it is essential to work slavishly toward an exact imitation of the colorimetic X, Y, and Z. Preliminary study has convinced me that quite good color matches can be made by the crude use of Wratten filters with the Clairex No. 5 material. What is required of a combined filter and photo-resistor is that it have a broadband, single-peaked sensitivity curve, falling off smoothly and monotonically away from the peak in both directions. It is important the the spectral colors be represented by three lines of numbers from the three filter-photoresistor com-binations that vary smoothly and systematically from one end of the spectrum to the other. Thus the spectral order is preserved along the boundary of the color space, and

the space itself is linear and homogenous and arises barycentrically from the spectrum. Two facts are immediately apparent. First, whatever the other properties of this space are, it is a continuous map of human color space. There can be no discontinuities or crossovers. Thus if a color becomes redder to us, it will also become redder to the device. Second, it is directly distortable into many different projections of itself simply by adding true neutral density filters to the color filters.
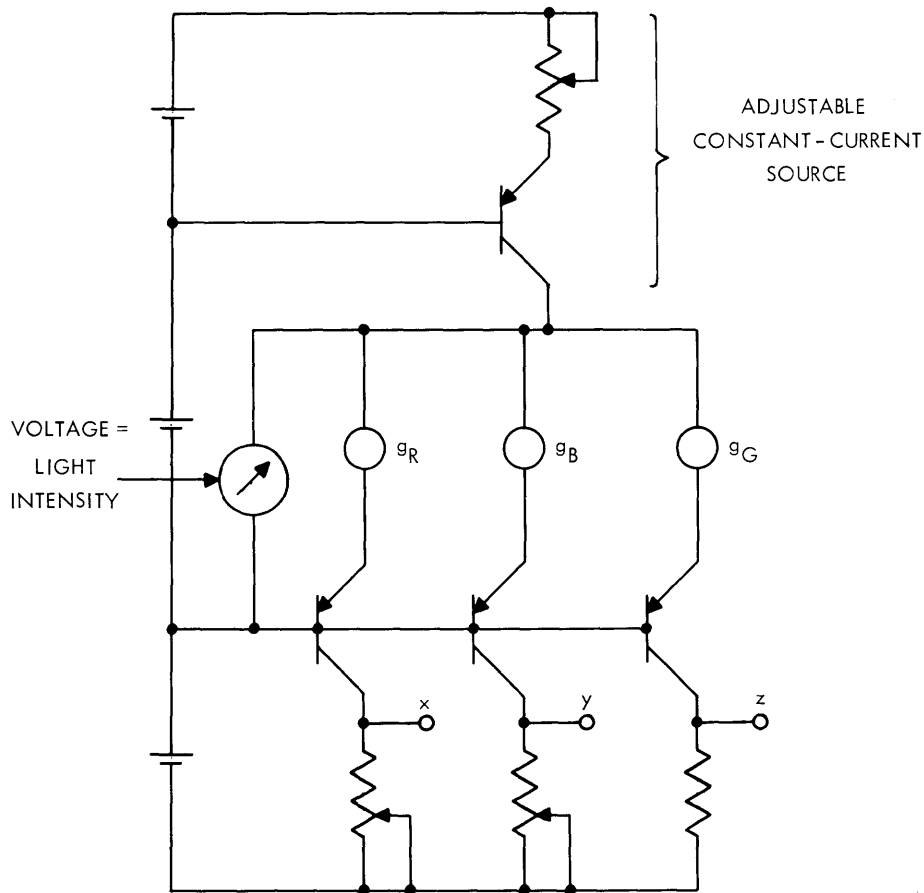

Fig. XXI-2. The Maggie A.

I should like now to show one of the variants of the device itself (see Fig. XXI-2). This version shows something that is like the Bezold-Brucke effect.

It seems to me that the general use of such quick and cheap computer analogues may be of use whenever one wants to construct a barycentric operation on a variety of data. So, for example, one might use strain gauges, thermistors, accelerometers, and all other such transducers that can be made to exhibit a conductance change that is a linear, or smooth and monotonic, function of the property to be sensed.

In general, when one is confronted with a spectrum of information, it is not a bad idea to look at that spectrum from three or more different views of the whole band. There are many advantages in so doing, as is clear from the comments on color vision. First, if you are comparing several different phenomena of different spectral composition, they have a certain distribution in the space relative to each other which tends to be preserved under translation, say, as with a continuously increasing bias between one end of the spectrum and the other. Second, phenomena that are undergoing a continuous change of spectrum can be distinguished sharply from those undergoing discontinuous changes.

Finally, it is occasionally of use to devise such a transformation on material which, at first glance, is thoroughly explored. Thus, for example, I see no reason why one cannot erect infrared color spaces and ultraviolet color spaces. But, more to the point, if, say, in cost accounting, or stock planning, one wishes to obtain a rough estimate and a variety of continuously variable factors determine the decision, the use of potentiometers and the circuit variant A (Fig. XXI-2), with as many potentiometers and transistors as are needed, would seem to be helpful.

One might feel that we have gone rather far afield from color vision. So we have. However, we now may ask whether such model-building is of help in thinking about physiology. I believe that it is, and I shall sketch a line of argument. Blue has a curious and anomalous position with respect to foveal color vision. It contributes little to the luminosity curve of the fovea; however, it has an enormous effect on perceived color. A mixture of yellow and blue that appears white remains white over a very considerable range of intensity. If, however, at all levels of brightness you check the blue alone and the yellow alone for brightness, you find that they do not change in the same way. The yellow seems to get continuously brighter, whereas the blue does not seem to get brighter at nearly the same rate beyond a certain low level, but the mixture stays the same color. This suggests that the brightness function and color function are not rigidly joined, and certainly that the brightness encoding probably does not precede the encoding of color. For the various reasons suggested by Stiles, Rushton, and others, I believe two things about the receptors. The first is the fact that the bleach of a pigment molecule in a receptor causes the same increment of response in the receptor, no matter how many other molecules are bleaching at the time, that is, the receptor process is linear with light intensity over a considerable range. If it were not so, if a cone were logarithmic or followed a power law with respect to rate of light absorption, it is hard indeed to see what sort of compensatory mechanism would give us the barycentric operation that yields the trichromatic laws. I think that one has to be reasonable about this. Unless one can guess what sort of compensatory function could be used and how it is generated, one must not postulate an arbitrary sort of transformation and leave it to the good old cortex to untangle. The

second is the fact that many, if not all, of the cones have all of the pigments in them. Stiles and Rushton separately have very good arguments for this. What convinced me, however, was my experimentation with very small spots of light. Using a spot of less than 0.1-mm diameter at a distance greater than 1 meter (thus, less in visual angle than the size of a cone) and flashing the spot with a strobe light at a low rate, I was unable to detect differences for a just threshold red light over time. That is, it is very unlikely that the spot will hit the same cluster of cones (I am not supposing that the image of the spot was a cone in diameter — the dioptrics of the eye forbids this) twice in a row. Since the spot was kept in focus, I felt that it was unlikely to occupy much more than a twenty-cone area till it fell off markedly in intensity. At any rate, the spot did not change in character, that is, hue, intensity or brightness, from moment to moment. This, I felt, implied that all cones usually reported on the same thing. (Furthermore, the only two colors that I could distinguish were red and a sort of bluish green, but the red was always far more saturated. Yellow appeared white, and blue itself could not be seen until the intensity was increased so far that it was unlikely to occupy a limited area on the retina at threshold. For the same intensity a green spot could be detected more easily than a red spot, but the color could be more easily assigned to the red spot.)

Suppose that all cones bore all three pigments but in different ways. Let us set up an argument. A quantum of light is absorbed by a pigment molecule that is thereby bleached. This bleaching, however, is no transduction unless it is coupled somehow to a power amplifier. There are many possible kinds of amplification. For example, the bleaching may set up a propagating chemical change in the vicinity (as in the photo-graphic process during development), and the resulting group of molecules is then released and diffuses to a place where, in turn, it can cause another change that leads eventually to a nerve firing somewhere. Or else the bleaching itself is an event that governs a membrane process so that an ionic current occurs, or an impedance changes, and so forth. I tend to believe, purely on faith, that the pigment molecules are adsorbed or in some way bound to the cone membrane, as some anatomists claim, and thus believe that the transduction is not mediated by several steps ending in a membrane change, but that the bleaching of a pigment molecule directly affects the membrane to which it is attached.

The way in which a continuous nerve membrane couples to itself from one patch to another is by virtue of the current flow between the patches, and the current is carried by ions. We may ask what sort of events are possible in the receptor end of the cone so that the cellular end and the pedicle are affected and can pass on information. If we believe that the information from the receptor is communicated electrotonically to the cell body and pedicle, and not by materials diffusing down the neck between cone and soma, then either current will pass from receptor to soma, or no event will be signalled farther on. Thus we enquire into what governs the flow of current through

membrane. There are two kinds of ions across a nerve membrane, those that are in equilibrium with the membrane potential and those that are not. (An ionic species is in equilibrium with a membrane potential when the potential between its activities on either side of the membrane equals the potential measured across the membrane.) If the resistance that a membrane offers to the passage of ions at equilibrium with the membrane potential (say K^+ or Cl^- in nerve fibers elsewhere) is lowered, then no current flows, and only the resistance to the flow of current changes. On the other hand, if the resistance to an ionic species not at equilibrium with the membrane potential is lowered, then it will tend to flow from the region of high activity on one side to the region of lower activity on the other side. This is an electric current through the membrane in one direction at the point where the resistance change has occurred, and diffusely back through the membrane in the other direction elsewhere. The membrane potentials of all other nerve elements which were measured are such that all ions of reasonable concentration and mobility (so that they are current carriers) are either at or close to equilibrium with it, or are far out of equilibrium with an activity potential in the opposite polarity to that of the membrane. I conceive that these events can occur at a transducer: either a nonequilibrium ion will be gated by an exciting event, an equilibrium ion or both. If only a nonequilibrium ion (say Na^+), is gated, current flows into the receptor and out through the rest of the membrane of the transducer and cell. If only an equilibrium ion (say K^+ or Cl^-) is gated, no current flows through the cell membrane. If both ionic channels are gated, the current that would ordinarily flow through the cell from the one is now attenuated by the shunting of the other. Thus we get "excitation" as current generation at a synapse or along a transducer membrane, and "inhibition" as a shunting, not itself capable of generating a signal but capable only of modifying excitations — essentially a divisive process. (I have commented elsewhere on the extension of this idea to dendritic trees.) However, in the cone, if we suppose that the bleaching of a green-absorbing molecule (Rushton's chlorolabe) is coupled to membrane in such a way that the bleaching step sets up a transient gating open of the Na^+ channel, then this pulse of current can be seen as a quantum of conductance change in the Na^+ channel so that it is linearly additive with similar quanta of g_{Na^+} from other sites in the same cone. Similarly, let us suppose that the red-absorbing pigment (Rushton's erythrolabe) is coupled in a similar way to K^+ or Cl^-, and so also is the blue-absorbing pigment (Rushton's cyanolabe). Do we not, then, have a good case (confected, it is true, out of no evidence) for which the device I have shown is a model? For in adjacent cones, only chlorolabe and erythrolabe need be reversed in their ionic-gating properties to generate the two necessary computations for the trichromatic theory. In another manner of speaking, in one cone, red light excites and both green and blue inhibit; in the other, green light excites and both red and blue inhibit. Thus blue can affect color independently of the way in which it affects luminosity, and its

effect on color would not depend on the subjective assessment of its brightness alone. (Willmer had something like this in mind.) You could probably make the followers of Hering very happy by having one cone in which red excited and green and blue inhibited, and another in which red and green both excited and only blue inhibited. The outputs would be what he requires for his "opponent" scheme. Any pair of different combinations work to generate the color plane, except those involving all pigments as all exciting or all inhibiting within the cone. Even blue can be made an occasional exciter without changing matters but giving it some luminosity function. The rules for combination by means of the nerve net can be made so explicit that only two adjacent cones have to be illuminated simultaneously for there to be no ambiguity between the colors. All other cones illuminated by the same light simply increase the resolution in distinguishing color, but do not change the color that is seen.

There are some distinct advantages in thinking that all cones bear all of the pigments. First, the dynamic range over which color can be held constant under change of brightness does not depend on carefulness in network design, and the operations are linear, as they should be. Second, the dynamic range of the receptor does not have to be as great and discriminable as it would have to be if each receptor had a separate pigment and displayed a linear output thereof. Third, it puts the color function before the luminosity function and thus is not dependent on it.

If broadband pigments are used, the vertical colors of the reference triangle must be imaginary. For, any pure spectral color will be represented by at least two numbers and a zero, while each of the vertices has one number and two zeros.

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Recommended Reading

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