VISUAL PERCEPTION

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It is important, in this regard, to point out that the red-absorbing pigment, if extracted from the retina, would not look red. If it were illuminated with white light, it would absorb the long wavelengths most strongly, and therefore reflect to the eye predominantly the middle and short wavelengths. When a mixture of middle and short wavelengths strike the normal eye, the observer calls this mixture bluish-green. Thus the red-absorbing pigment has a bluish-green color, and likewise, the green-absorbing pigment has a purplish color and the blue-absorbing pigment a reddish color. Similarly, "visual purple" (another name for rhodopsin) is a blue-green absorbing pigment (that is, it absorbs maximally at a wavelength of 507 nm; this wavelength, when exposed at intensities great enough to stimulate the cones, is called bluish-green). The pigment is called visual purple because that is the color of the pigment when seen under white light.

TETRACHROMACY

According to the evidence from microspectrophotometry, the normal retina contains cones with three different spectral sensitivity curves, and each of those curves is different from the spectral sensitivity curve of rhodopsin, the rod pigment. Therefore, the normal retina contains *four* classes of receptors with different absorption spectra. Such a retina should then be expected to be tetrachromatic, rather than trichromatic.

Much of the data on matches between mixtures of wavelengths has been collected when the patches to be matched are small, and under these circumstances (when the patches are no larger than about 2° in diameter), normal vision is exactly trichromatic. This is to be expected if the subjects fixate the two patches in turn, and make their matches on the basis of the activity resulting from each while it is being fixated, since there are very few rods in the central 2° of the retina. However, when the patches are larger than 2°, tetrachromacy should be expected. The fact that trichromacy has generally been reported even for large fields has been taken as evidence that the rod system simply does not operate when the intensity of the field is great enough to stimulate the cones. It has been hypothesized, for example, that the rods are inhibited when the cones are active. However, when the measurements are made under special conditions, normal human vision is, in fact, tetrachromatic for large fields.

To distinguish between trichromacy and tetrachromacy, measurements must be made with great care. Very few of the published measurements have used sufficiently sensitive procedures. The technique that is usually followed in collecting data on wavelength matches is simply to present the subject with two patches illuminated by different combinations of wavelengths of light and ask him to adjust the intensities of some of the components until the two patches match, that is, look the same. The subject is almost never tested to determine whether or not he can *discriminate* between the two patches. It is quite possible that a subject will say that two patches look alike even when the effects of the two patches on his visual system are different enough to permit him to discriminate between them if he is asked to do so. This is an extremely important point. The logic (explained in Chapter VIII) by which the color mechanisms of the visual system can be deduced from wavelength mixture data depends critically upon the assumption that, when two patches are "matched," their effects on the visual system as a whole are *identical*, and that when two patches have identical effects on the visual system, they cannot be discriminated.[8] The number of color systems in the retina *cannot* be deduced from wavelength matching data taken simply by finding mixtures of wavelengths that "look alike." It must either be demonstrated or assumed that the stimuli are indiscriminable, and it is a very poor (almost always incorrect) assumption that, when a subject sets two patches to look the same, he will be unable to discriminate between them. If he is given some training, he can usually distinguish between wavelength mixtures that he had previously adjusted to look alike, no matter how careful he was in his original adjustments.

To reach firm conclusions about retinal color systems from wavelength mixture data, the experimenter should always make the final adjustments himself, adjusting the intensities until the subject *cannot learn to discriminate* between the patches. However, this procedure is so time consuming, and the logical arguments that show why it is required are so widely ignored, that experimenters have rarely collected wavelength mixture data in that way.

When large stimulus patches are used, and only three intensity adjustments are permitted, the subject will often report that the patches match well in the regions where he is looking but do not really match very well in the parts that fall on the periphery of the visual field. Mea-

[8]In essence, the logic is as follows: You wish to test the physiological theory that there are only three sets of receptors (with different action spectra), all operating at the same time. If that theory is correct, and a subject is presented with two patches of light containing mixtures of four wavelengths, it must be possible to find intensities for three of the wavelengths such that the two patches will have *identical* effects upon his system as a whole. If the two patches have identical effects, the subject cannot discriminate between them. Therefore, the theory is disproved if the subject can discriminate between the patches at all intensity settings. (There is no set of operations by which this theory, or any theory, can be proved.)

surements by Bongard *et al.* (1957), using a careful procedure in which differences far from the fovea were made more easily noticeable, indicate that the normal subject really is tetrachromatic for large fields. Those measurements did not employ discrimination testing procedures, but at least the stimuli were arranged in such a way that peripheral differences between the patches were more noticeable, and the subjects were instructed not to ignore them. The experimenters found that the normal subject is trichromatic for patches smaller than 2° in diameter, but that he requires four intensity adjustments to equate two larger patches. Thus it is evident that the rods are not inhibited and do contribute to wavelength discrimination, at least under their conditions of measurement. They did find, however, that, even for large patches, three intensity adjustments were sufficient to provide reasonably good matches. In other words, for practical purposes, such as designing color television sets, the trichromatic data in the literature are only slightly in error, and may be taken as a useful description of normal color vision.

EVALUATION OF THE ASSUMPTION THAT ALL ABSORBED QUANTA PRODUCE IDENTICAL EFFECTS

While the probability that a quantum will be absorbed certainly depends upon the relationship between the nature of the pigment molecule and the wavelength of the quantum, most of the preceding discussion of color vision depends heavily upon the assumption that, once a quantum is absorbed, it will have an effect on the molecule that is the same regardless of the wavelength of the quantum. That assumption will be evaluated in this section.

It is firmly established that all lights at near-threshold intensities look the same when presented to the periphery of the dark-adapted eye, regardless of their wavelengths. That is, the dark-adapted eye exhibits monochromacy. (If the lights are presented to the fovea, long-wavelength stimuli look colored because, at long wavelengths, the cone threshold is somewhat lower than the rod threshold. When the stimuli are restricted to the rods, however, there is no wavelength discrimination.) Specifically, if any two lights of different wavelengths are adjusted in intensity so that they produce equal numbers of quantal absorptions, the two lights will be indiscriminable (other factors, e.g., size of test patch, being equal). Therefore, the information contained in the wavelengths of the quanta is certainly lost somewhere in the visual system.

Similarly, the trichromacy of normal vision can only be reconciled with the presence of three kinds of cone pigments if it is true that wave-