

COLOR VISION

by Saul M. Luria

PHYSICISTS, PSYCHOLOGISTS, PHYSIOLOGISTS and artists—not to mention paint manufacturers—have all played substantial roles in the study of color and color vision. Many disparate points of view have resulted in great cross fertilization but, not surprisingly, some confusion as well. One confusion is the dichotomy of physical stimulus and sensation, that is, color perception. Several different theories have attempted to explain the relation between the two, the two major ones being those called “trichromatic” and “opponent-process.” Meanwhile observable facts have been determined by many types of measurement: color mixing, wavelength discrimination, spectral sensitivity and studies of color blindness. We do not know all the answers yet, but apparently all the major theories have their own validities at different levels of perception.

Stimulus and sensation

Elementary physics and psychology both teach that electromagnetic radiation has three parameters: frequency, amplitude and complexity and that there is direct correspondence between changes in these parameters and the perception of the three attributes of color: hue, brightness and saturation. Hue is colloquially called “color.” Brightness is defined as the subjective impression of the intensity of stimulation. Saturation refers to purity or depth or richness of the color. There has been some confusion in relating saturation to the physical stimulus. It has been defined both in terms of bandwidth or homogeneity of the stimulus and in terms of the amount of white light that is mixed with the wavelength in question. The association between physical and psychological dimensions

(which I discuss more fully in the box on page 35) becomes so firmly fixed in the student’s mind that he may find it difficult to resolve such questions as whether or not a bolt of lightning produces a light (or a falling tree produces a sound) if there is nobody around to witness it.¹

Hue is basically related to frequency, but changes in the hue of most stimuli also result from changes in the intensity of stimulation. This is called the Bezold-Brücke phenomenon. With increases in intensity, only three hues in the spectrum remain invariant, those at wavelengths around 475, 505, and 570 millimicrons. Yellowish-red and yellowish-green hues become more yellow and reddish-blues and greenish-blues become bluer. Changes in hue also result from changes in saturation. This is known as the Abney effect; it appears that yellow-reds become redder with increasing saturation and blue-greens become bluer.

Similarly, although increases in brightness result from increases in the energy of a given wavelength, very marked changes in brightness for a given energy level result from changes in wavelength, or the homogeneity of the stimulation. The reason, of course, is that the eye is maximally sensitive to radiation around 550 millimicrons and far less sensitive to radiation around 400 or 700. This function is called the “luminosity” curve.

Finally, changes in saturation occur not only with changes in the homogeneity of stimulation, but for a given bandwidth it changes with wavelength. Saturation is maximal for stimuli at the ends of the visible spectrum and minimal at around 580 millimicrons in the yellows. Moreover, changes in saturation occur with changes in intensity. This is called the Purdy effect. As the brightness of a color increases, its saturation increases up to a certain point and then decreases until no color may remain and only the sensation of brightness is left.

Apart from these facts, the color produced by

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Correspondence between physical stimulus (frequency, intensity, complexity) and sensation (hue, brightness, saturation) is neither obvious nor simple. Many theories offer explanations, but none has been entirely satisfactory. Now it appears that all of them have relevance, and color phenomena are being understood.

a given stimulus can be made to change simply by changing the viewing conditions or the immediately prior history of exposure of the observer; variations in the brightness or hue of the background can be made, or the observer can be adapted to various lights before he makes his observations.² There is, thus, a sharp distinction between stimulus and sensation, and it may not be obvious what sensation a given stimulus will produce.

The most publicized and dramatic demonstrations of the lack of strict correspondence between stimulus and sensation have been those of Edwin Land.³ He has photographed subject matter on black-and-white film through first a red and then a green filter. When the negatives are projected in registry through a red filter and no filter, respectively, the original scene is reconstituted in what seems to be almost full color. It was quickly pointed out⁴ that this phenomenon was first demonstrated more than half a century ago. Probably almost all psychologists hold that Land's results are a complex example of what is called "simultaneous color contrast" or "spatial induction."⁵ Land himself, in rediscovering the phenomenon, believed that it called into question all classical color theory.

Theories of color vision

A theory of color vision must account for a wide variety of phenomena:

- *Three-component specification.* Only three colored component lights are necessary and sufficient to specify any color for the normal observer.

- *The facts of color mixture,* particularly as summarized by "Grassman's Laws" which state that (a) when equivalent lights are added to (or subtracted from) equivalent lights, the sums (or differences) are equivalent, (b) lights equivalent to the same light are equivalent to each other, (c) for every color there is a "complementary"

color which, when mixed with it in the right proportion, gives white or gray, although the mixture of noncomplementary colors gives an intermediate color.

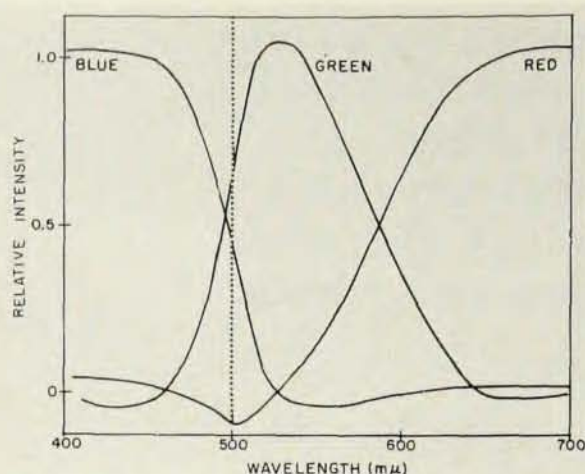
- *Hue discrimination,* which is poor at the ends of the spectrum and is best around 480 and 580 millimicrons. Theory must also account for dif-

Sound without Hearing? Light without Sight?

Does a falling tree make a sound if no one is around to hear it? Does a bolt of lightning produce a flash if no eyes receive the light waves?

Vasco Ronchi has discussed the problem at some length.¹ Dealing first with the example of sound, he writes, "Sound is without doubt a subjective phenomenon. Outside the mind there are vibrations. These, however, are not sound or noise, but a *silent* motion. Only when these vibrations have been received by an ear, transformed into nerve impulses, and carried to the brain . . . is the sound created . . ." Ronchi notes that when it was found that heat is a form of kinetic energy, physicists thenceforth ignored the sensations of warmth and cold, and heat became a topic of mechanics. Similarly, physicists should have avoided talking about sound and color and concerned themselves only with acoustic vibrations and radiation; for to identify vibrations with sound leads students to believe that the vibrations are sound.

Ronchi suggests that physicists did not want to prevent these misunderstandings because they did not want to admit that their world was without sound or light. It is not quite clear whether he is referring to their psychological or professional world. In any event, even if care is taken to make the distinction between the physical and psychological dimensions, the fact is that it is still inaccurate to say that there is a strict correspondence between frequency and hue, amplitude and brightness, and complexity and saturation. These relationships are, of course, the basis of color but it is, nevertheless, possible to change, more or less, each one of the perceptual attributes by changing any of the physical parameters.



THREE-COLOR MATCHING. Persons with normal vision use these intensities to match spectral colors on horizontal axis. Thus dotted line shows values used to match 500 millimicrons. Values below zero show that color is applied to standard. Curves are from reference 22. —FIG. 1

ferential sensitivity to spectral radiation.

- *Various phenomena* such as the psychologically unique hues, the Bezold-Brücke effect, contrast and induction effects.

- *Defective color vision.* There have been two major theories of color vision and two important ancillary groups of theories. The most influential theory has been the "trichromatic" one based on the ideas of Thomas Young and elaborated by Helmholtz. The main alternative theory has been the "opponent-process" theory proposed by Hering and recently quantified by Hurvich and Jameson.⁶ A third and important group of theories, called "zone" or "stage" theories, have attempted to combine the former two. The most detailed one was proposed by G. E. Müller. Finally, at times polychromatic theories have been proposed in place of the trichromatic theory.

According to the trichromatic theory, the eye has three kinds of receptors. Each kind contains a photochemical that is maximally sensitive to one of the three fundamental colors, red, green or blue. All sensations are simply compounded of varying amounts from these three systems; white arises from equal excitation of all three, and yellow, from equal excitation of red and green.

The trichromatic theory rests squarely on early color-mixture experiments showing that any color (the standard) can be mathematically represented as a mixture of three colors (called primaries) that are reasonably spaced throughout the spectrum (figure 1). This principle is sometimes somewhat erroneously rephrased to say that any color can be *matched* by a mixture of three colors. That this is not quite true has somewhat detracted

from the theory. A mixture of colors always results in some loss of saturation, so that a spectral color can never be matched by a mixture. What must be done is to desaturate the spectral color with one of the primaries. In effect, then, two mixtures of two colors each are matched

$$a\lambda_{st} + b\lambda_1 = c\lambda_2 + d\lambda_3$$

A feature of the theory is that should we wish to know what proportions of another set of primaries would have been needed, this can be calculated from the first set of results, and so it is not necessary to make new observations. But this strength is at the same time, from a psychological point of view, a great weakness. For there have been two aspects of the theory; in addition to its mathematical aspect, there is also the statement that there are three types of receptors in the retina, each maximally sensitive to a given wavelength. The trouble is that since there can be an infinite set of mathematical primaries, it is impossible to know from the theory which set reflects the retinal physiology. It has been necessary, therefore, to try to specify the "real" primaries from an analysis of various kinds of psychophysical data.

Color blindness

One of the main approaches has been the study of individuals with defective color vision. According to the theory, defects occur when one, or more, of the three receptors or its pathway is for some reason, not working, resulting in a corresponding loss of sensitivity. And since white results from all three receptors, there should presumably also be a loss in brightness sensitivity. Let us briefly review defective color vision.

People with color-vision defects are generally called "color-blind," but this term is somewhat unsatisfactory, since it implies that they cannot see any color at all. In fact, although some form of defective color vision is found in about 8% of white males and 0.5% of white females, total color blindness (achromatopsia or monochromatism) is very rare.⁷

There are three main methods of studying color perception. The first is the matching of color mixtures. Since, as we said, color normals require three primaries to complete a match to a standard, they are called *trichromats*. Many color defectives, however, need to dispose only two primaries to complete a match; they are, therefore, called *dichromats*. Those few people who are completely color blind, the *monochromats*, need only one primary, of course; they can match any color with any other color provided they can equate

the brightnesses. (Another group of people, called "anomalous trichromats," need three primaries, but, as the name implies, make different matches than normals.)

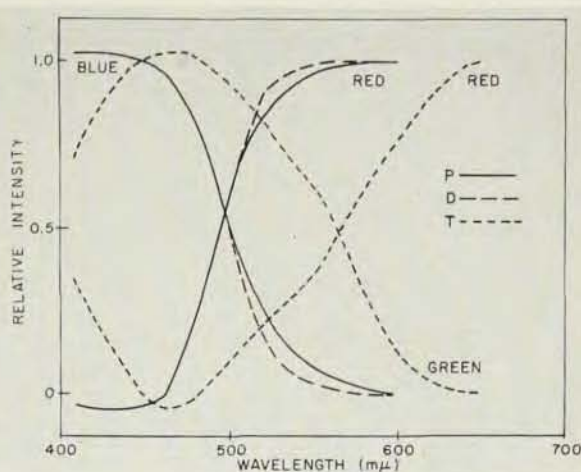
As theory demands, the color-mixture curves of the dichromats—with whom we are most concerned—are regarded as falling into three classes, called "protanopia," "deutanopia" and "tritanopia." But the curves for the first two groups of people, who are both red-green blind, are extremely similar. People in the third group, who are relatively few, are yellow-blue blind (figure 2).

The second method is to measure wavelength-discrimination functions. Again the curves fall into three classes, but the protanopic and deutanopic curves again differ only slightly (figure 3), despite the argument that protanopes should have much better color vision than deutanopes.⁸

The third method, measuring spectral sensitivity, separates the deutanopes and protanopes decisively: the latter are much less sensitive to the long (red) wavelengths. Trichromatic theory predicts that the other two classes should also show some loss of sensitivity, but it is not certain that the tritanopes show a loss in the blue, and it appears that only some deutanopes show a loss in the green. It is possible to explain why some deutanopes do not show a loss in the luminosity curve, however, by assuming a fusion of the red and green systems rather than a loss of the green. Although other difficulties with the theory can be overcome by making other additional assumptions, the psychophysical data never led to agreement on which are the "real" primaries.

Another shortcoming is that it is not obvious from the theory what sensations will be experienced by either normals or color defectives. For example, since protanopes can discriminate only in the blue-green region of the spectrum and there is loss of sensitivity to the red, we would expect them to experience blues and greens. In fact, they see blue and yellow.⁹

A similar theoretical deficiency with regard to normal color perception provided the impetus for the major theoretical opponent of the tristimulus theory. Some colors are obviously composed of, or partake of, other colors; orange, for example, is composed of red and yellow, and purple is composed of blue and red. At the same time, some colors do not appear to partake of other, more fundamental colors. They are "unique". All color normals, when asked to select such colors, choose four: a blue around 470 millimicrons, a green around 500, a yellow around 570, and a red around 700 mixed with a little violet.¹⁰

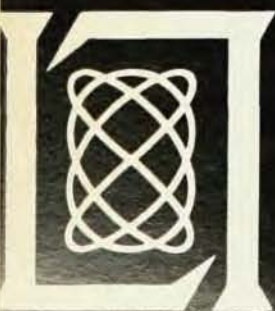


DEFECTIVE MATCHING. Persons called "dichromats" match any standard with only two primary colors. Curves show intensities that three kinds of dichromats use to match spectral colors. Protanopic and deutanopic curves are from reference 23; tritanopic curves are from reference 24. —FIG. 2

Obviously, it was difficult to understand why a visual system that is presumably based on three receptors should lead to the perception of four unique colors. There are several other visual phenomena that are clearly related. The unique colors do not change their hue with changes in intensity, as do the other colors. The visual system often appears to function in terms of pairs of colors, as evidenced in mixtures of complements to give gray; in the phenomenon of spatial induction, when a given color induces its complement into an adjacent gray area; in negative after-images, when the removal of a given color after prolonged fixation results in the sensation of its complement; in acquired impairments after disease, when individuals become insensitive to pairs of colors. When stimulus magnitude is very small, discriminations involving yellow and blue become worse than those involving red and green.

Opponent-process theory

Such considerations led to the opponent-process theory of color vision. This theory holds that yellow must also be counted a primary color, making four altogether. In view of the complementary relation between red-green and yellow-blue shown by color mixing, spatial induction and after-images, it assumes that these four colors, together with black and white, form three pairs of unique sensory qualities. Moreover, since we never experience a reddish-green or a yellowish-blue (in contrast, for example, to yellowish-red or greenish-blue) the members of each of the three pairs are held to be mutually exclusive, or "opponent," sensory qualities. The theory postulates that



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these qualities are directly associated with physiological processes that are also opposite in nature.

When the opponent-process theory was first proposed, the nature of these antagonistic physiological processes was unknown, and, primarily for this reason, it attracted far less support than the trichromatic theory; the notion of opponent physiological processes was criticized as being bad physiology. But the greater parsimony of the trichromatic theory as well as the powerful foundation of three-color mixture also helped maintain trichromatic supremacy.

Nevertheless, because of the shortcomings of trichromatic theory, a zone, or stage theory was soon proposed to harmonize it and tetrachromatic (or multichromatic) theories. G. E. Müller originally proposed the most detailed version, which has since been treated quantitatively by D. B. Judd.¹¹ These theories postulate that there are several stages of activity in the visual pathway. The trichromatic mechanism operates at the first stage, the retina. Activity here produces responses in the second stage, and so on. It is in the later stages that an opponent type of mechanism might be found. There has been relatively little discussion of the stage theory apparently because most investigators have paid such strong allegiance to one of the two main theories.

Finally, there have been several suggestions that a polychromatic theory is necessary. H. Hartridge⁸ advanced the idea that seven color receptors are necessary to explain that a very small white stimulus will turn different colors at different positions on the retina. More recently, Stiles concluded that one might need five or seven mechanisms.¹²

Recent findings

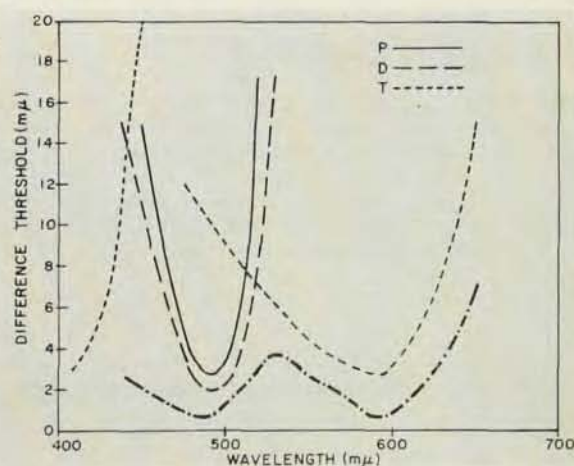
A series of physiological studies in recent years have enormously elucidated the mechanisms of color vision. This advance may be said to have been started by R. Granit.¹³ He stimulated the eyes of various animals with diffuse white and colored lights, and, using microelectrodes, recorded the resulting electrical responses in different optic-nerve fibers and ganglion cells of the retinas. (If we consider the photoreceptors to be the first layer of the retina, the ganglion cells are the third layer in the chain leading to the brain.) Plotting the responses as a function of wavelength, Granit found in many organisms, first, that some curves were broad and some narrow, and second, that the wavelength producing the greatest response varied with different cells. For example, most of the units studied in the light-adapted cat's eye produced narrow curves peaking at about 450,

540, and 610 millimicrons (which is interesting because it is unlikely that the cat has good color vision¹⁴), although a broad curve peaking at 560 millimicrons was also found. Granit thought that the broad curves resulted from the combined action of several narrow curves, and he was able to explain a number of perceptual phenomena in such terms. The relevance of these findings to trichromatic theory is obvious, but certain aspects of his findings appeared to support the opponent-process theory and so his findings have been said to be neutral as to theory. What should be noted is that when Granit got "on" responses from one light, he got them from all lights.

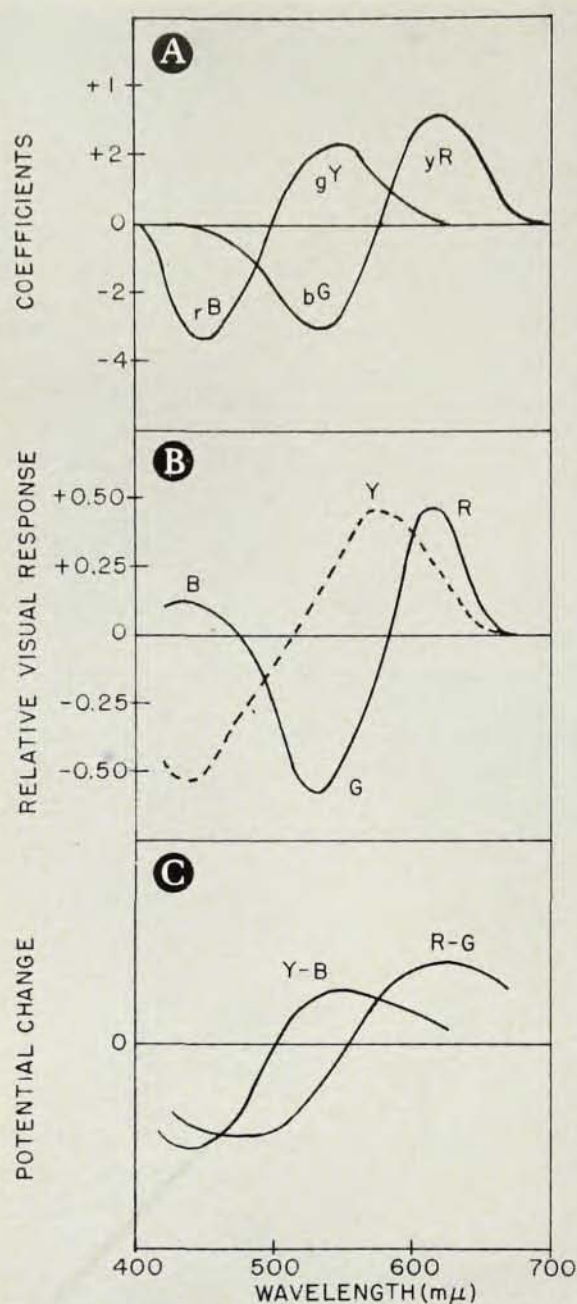
The next big step was taken by G. Svaetichin¹⁵ through microelectrode studies of cells (probably horizontal cells a layer away from the photoreceptors) in the retina of fish known to have color vision. Although he sometimes obtained a polarizing (increased intracellular negativity) potential in response to any wavelength, Svaetichin also obtained polarizing responses with one stimulus and depolarizing responses with another stimulus. The latter curves were of two classes: a red-green curve showing depolarizing responses for wavelengths up to about 580 millimicrons and polarizing responses thereafter; the yellow-blue curve showed polarizing responses for wavelengths up to about 580 millimicrons and depolarizing responses thereafter. Later, H. G. Wagner, E. F. MacNichol and M. L. Wolbarsht¹⁶ found the same phenomena in the retinal ganglion cells of other fish.

Support for opponent process

Here it is obvious what support these findings gave to the opponent-process theory; the graphical



WAVELENGTH DISCRIMINATION. Each curve indicates difference required for an observer to differentiate. Dot-dash line at bottom is for normals (but should probably be scaled differently). Other curves are for dichromats. (P and D curves are from reference 23, T curve from reference 24). —FIG. 3



ZONE THEORY postulates several stages of activity along visual pathway, and comparison of these findings supports it. Part A shows theoretical sensitivity curves for second stage of Müller's theory as derived by Judd.¹¹ In B are spectral distributions of paired chromatic responses determined experimentally for one subject.⁶ C shows local potential changes from electrode recordings of a vertebrate retina.²⁰ —FIG. 4

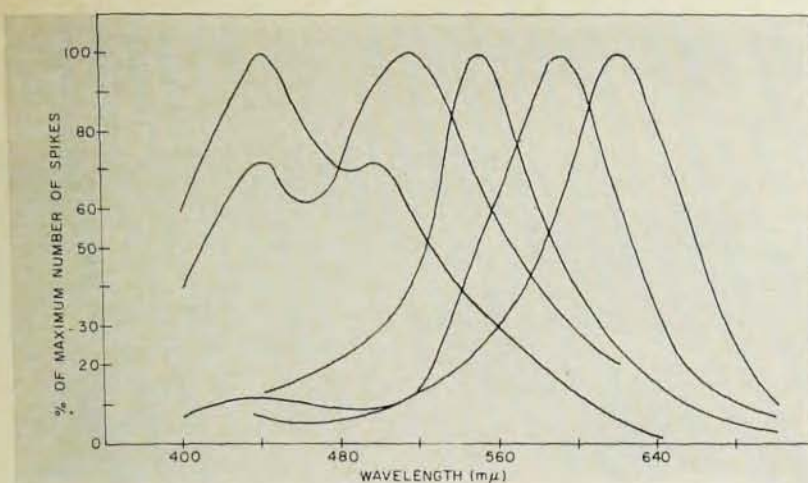
representation of the results could not be more striking. Figure 4 compares the theoretical curves derived by Judd for the second stage of Müller's theory, the spectral distributions of the paired chromatic responses determined by Hurvich and Jameson for one of their observers, and some electrode recordings obtained by Svaetichin and MacNichol.

Next, R. DeValois¹⁷ explored the responses of the lateral geniculate body (LGB) of the macaque monkey, which is known to have good color vision. The LGB is some sort of way-station after the optic chiasma (where some of the optic-nerve fibers cross) and just before the visual area of the cortex. Some cells in the LGB give both "on" and "off" responses which are a function of wavelength of stimulus. (An "on" response is an increase in the activity of the cell when it is stimulated; an "off" response is an increase in activity when the stimulation ceases.) DeValois found that some cells were stimulated by red light and inhibited by its cessation; blue light, on the other hand, would inhibit these cells, which would, however, respond at its cessation. Other cells behaved oppositely.

Despite this onslaught, few supporters of the trichromatic theory were seen to lose heart. They steadfastly maintained that no matter which opponent-process details might eventually be included, the trichromaticity of vision is a fact and the final account would have to be trichromatic in nature. Some psychologists felt, however, that it was the trichromaticity of the physical stimuli rather than that of psychological sensations that was indisputable. Others suggested that the trichromatic nature would refer to the three opponent processes, white-black, yellow-blue, and red-green.

But the trichromatic theory has gained additional support as dramatically as did its rival. This has come from microspectrophotometric studies of individual photoreceptors. The first studies were of fish eyes and indicated existence of three photopigments with narrow response curves. Then W. B. Marks, W. H. Dobbelle, and MacNichol¹⁸ and P. K. Brown and G. Wald¹⁹ simultaneously reported recordings from individual photoreceptors in a human eye studied a few hours after death. Both teams of investigators obtained three sets of curves. The former reported peaks at about 445, 535, and 570 millimicrons; the latter at around 450, 525, and 555. Both sets of results appear to indicate, then, that there are three kinds of (daylight) receptors in the eye, each with predominantly a single pigment that is maximally receptive to one of three different parts of the spectrum.

Finally, two new findings should be noted. We have already mentioned the findings of DeValois that supported the opponent-process theory; he has also found some cells that give only "on" responses and show a sizable response to only a relatively narrow portion of the spectrum. He has



NEW FINDINGS offer further support of zone theory. Curves show average responses of certain cells that give only "on" responses and give sizable responses only to narrow portions of the spectrum. An "on" response is an increase of electrical activity when a stimulus is applied. An "off" response is an increase of activity when stimulus is removed. R. DeValois¹⁷ has reported five functions, two of which have a secondary peak.

—FIG. 5

reported five such functions, two of which have a secondary peak (figure 5).

Finally, V. O. Andersen and his co-workers²⁰ have reported electrode recordings from what they call "single units" in the visual area of the monkey cortex that respond to rather narrow portions of the spectrum.

Much to be done

In conclusion, it now appears that all the major theories have been vindicated to some extent and that the final explanation of color vision may well rest on the trichromatic basis at the receptor level, on the opponent-process mechanism at several succeeding levels and on some sort of polychromatic mechanism at the higher levels.

Much, of course, is left to be done. Techniques have been developed for measuring the absorption curves of pigments in the intact human eye,²¹ and they are beginning to provide important data. We would like more recordings from human receptors and from single cortical cells, and it is of interest to determine whether or not the processes operating at more peripheral stages in the system are maintained in the cortex. A major shortcoming is the lack of recordings at the various stages in the system from the same organism. Great insights have been afforded by the various comparative data that we have, but something is to be desired when we must try to reconstruct the mechanism of the visual system with, for example, data from the photoreceptors in man, the horizontal cells of teleosts, the ganglion cells of goldfish, the lateral geniculate body of a monkey and the cortex of the cat.

If it is too early to give the final description of the mechanism of color vision, it is not too soon to pay tribute to the astonishing insight of men like Young and Hering who so long ago grasped what the essentials of the mechanism must be.

Opinions and assertions in the article are the author's private ones and not to be construed as official or as reflecting the view of the Navy Department or the Naval Service at large.

References

1. V. Ronchi, *Optics: The Science of Vision* (New York University Press, New York, 1957) pp. 16, 17.
2. H. Helson, *Am. J. Psychol.* **60**, 1 (1947).
3. E. H. Land, *Proc. Nat. Acad. Sci.* **45**, 115; 636 (1959).
4. G. Walls, *Psychol. Bull.* **57**, 29 (1960).
5. J. A. S. Kinney, *Vision Res.* **2**, 503 (1962); *J. Opt. Soc. Am.* **55**, 731 (1965).
6. L. M. Hurvich, D. Jameson, *Psychol. Rev.* **64**, 384 (1957).
7. F. H. C. Marriott in *The Eye*, vol. 2 (Hugh Davson, ed.) Academic Press, New York, 1962) p. 282.
8. H. Hartridge, *Recent Advances in the Physiology of Vision* (The Blakiston Co., Philadelphia, 1950) p. 260.
9. D. B. Judd, *J. Opt. Soc. Am.* **39**, 252 (1949).
10. F. L. Dimmick, M. R. Hubbard, *Am. J. Psychol.* **52**, 242; 348 (1939).
11. D. B. Judd, *Doc. Ophthalmol.* **3**, 251 (1949).
12. W. S. Stiles, *Proc. Nat. Acad. Sci.* **45**, 100 (1959).
13. R. Granit, *Sensory Mechanisms of the Retina* (Yale University Press, New Haven, Conn., 1947) p. 310f.
14. J. A. Sechzer and J. L. Brown, *Science* **144**, 427 (1964).
15. G. Svaetichin, *Acta Physiol. Scand.* **39** (Suppl. 134) 17 (1956).
16. H. G. Wagner, E. F. MacNichol, M. L. Wolbarsht, *J. Gen. Physiol.* **43** (part 2), 45 (1960).
17. R. DeValois, *J. Gen. Physiol.* **43** (part 2), 115 (1960).
18. W. B. Marks, W. H. Dobbie, E. F. MacNichol, *Science* **143**, 1181 (1964).
19. P. K. Brown, G. Wald, *Science* **144**, 145 (1964).
20. V. O. Andersen, B. Buchmann, M. A. Lennox-Buchthal, *Vision Res.* **2**, 295 (1962).
21. W. A. H. Rushton, *J. Physiol.* **168**, 345 (1963); **176**, 24 (1964); H. Ripps, R. A. Weale, *Vision Res.* **3**, 531 (1963).
22. W. D. Wright, *Trans. Opt. Soc. (London)* **30**, 141 (1928-29).
23. F. H. G. Pitt, *Med. Res. Council Spec. Report*, Series No. 200 (1935).
24. W. D. Wright, *J. Opt. Soc. Am.* **42**, 509 (1952).
25. G. Svaetichin, E. F. MacNichol, *Ann. N. Y. Acad. Sci.* **74**, 385 (1958).