

# The "looks" of Helmholtz<sup>1</sup>

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A biographical sketch (with picture) of Helmholtz is given along with a description of his invention of the ophthalmoscope and the development of his trichromatic theory of color vision. Modern findings concerning the visual receptors for color vision are then reviewed. These include: electron microscopic studies of the retina, wavelength absorption spectra of single cone receptors, response potentials recorded from such receptors, bleaching spectra of cone pigments, electroretinograms showing components triggered by cones and matched by human psychophysical data, and finally the derivation of human color response functions from retinal potential waves produced by alternating stimulation with lights of different wavelengths.

In choosing my title, "The Looks of Helmholtz," I have wished to emphasize three of the main intentions of this talk. First, to commemorate with you the physical appearance of the man, together with a brief reference to his personality as described by his friends and biographers. Second, to recall the insatiable curiosity that drove him to look into so many of the unsolved scientific problems of his day. Finally, to rejoice in the fact that some of the findings in experimental laboratories of our own day continue to provide confirmation of the far-seeing theories that Helmholtz proposed or developed.

Of the many portraits of Helmholtz, I have chosen this familiar one to remind us of how he looked (Fig. 1). Good health and vigor characterized most of the 51 years of his scientific productivity, from 1842 to 1893. In early childhood he had been frail, and he was not permitted to enter school at the usual age. His father, a school-master, saw to it that he had interesting games and toys to play with. His special favorite was a set of wooden blocks with which he spent many hours building structures having various geometrical forms. Of his school years there is some lack of agreement among biographers. Koenigsberger (1906), a mathematician and a close friend of Helmholtz, writes: "As regards his studies, he was by no means devoted exclusively to the exact sciences, for the first school report in the first class testifies to a fairly level interest in all branches of his studies, his progress in Latin, Greek, Hebrew, religious instruction, mathematics and physics being characterized as good, and history and geography as excellent . . ." (ibid. p. 10). His translations of sixty lines of the *Hecuba* of Euripides was marked "very satisfactory"; his French version of a piece of two columns called *Die Katakomben* was "excellent"; while the Hebrew professor gave him the highest praise for his Latin commentary on Deuteronomy ix. 1-3 "...thanks to

the ceaseless efforts of his parents, whose intellectual standard was ever set to high ideals, he was filled with passionate enthusiasm for music and poetry, as well as for art and science." In Boring's *History of Psychology* (1950), however, we find the following summary, "He did not do very well in his school studies, but his apparent mediocrity seems to have been due to his independence of thought rather than to any lack of ability..." And later: "He had no gift for languages. His father tried to interest him in poetry and even to train him in writing poetry, but without much success."

Whichever version of the facts may be true in regard to his early progress, there is no doubt that in his years at the Potsdam Gymnasium he developed a talent for individual exploration of problems in mathematics, optics and biology. His father could not afford to provide him with a university education in physics, the subject that most appealed to him; instead, he arranged for his son to go to medical school in Berlin on a state scholarship that was awarded with the understanding that he would serve a term as a medical



Fig. 1. Hermann Ludwig F. von Helmholtz.

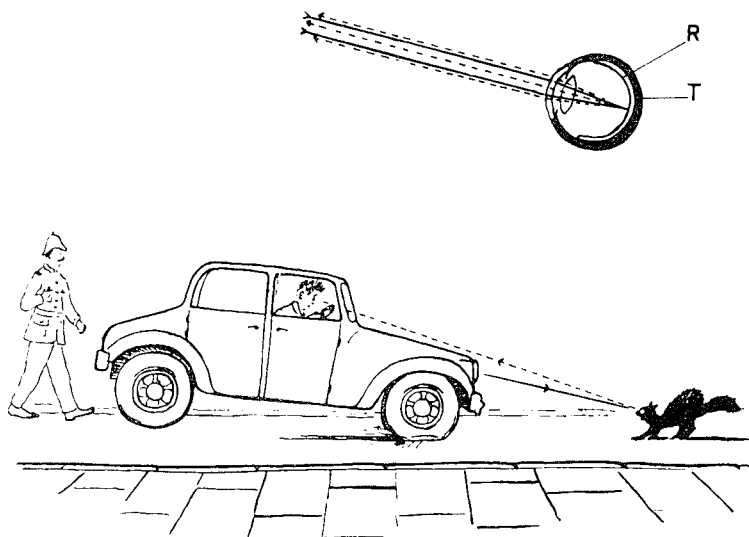


Fig. 2. Light reflected by tapetum (T) through retina (R) of a cat. (From Rushton, W. A. H. *Visual pigments in man*, 1962. Courtesy of Charles C Thomas, Publisher, Springfield, Illinois.)

officer in the Prussian army. In Berlin, Helmholtz pursued the medical curriculum, but he also attended lectures by leading scientists of the time. The most influential of these was Johannes Müller (1838), whose doctrine of specific nerve energies was a particular stimulation for Helmholtz. A thorough grounding in the physical sciences and in mathematics were a part of the medical program in Berlin. Thus Müller, and his pupils Du Bois Reymond, Brücke and Helmholtz, were physicist physiologists. They rejected the prevalent animistic dogma that living processes are metaphysical, and hence beyond the scope of science. They, and Helmholtz was foremost among them, looked for physical explanations for every phenomenon of nature, from the propagation of the nerve impulse to the perception of color and tone.

Biographers of Helmholtz (Koenigsberger, 1906; McKendrick, 1899; and Hall, 1912) portray him as an eminently fair and sensible man in relationships with his family, friends, and intellectual associates. He was kindly in his manner, rather than warm or outgoing. But all agree with Helmholtz' own appraisal of his most dominant characteristic, namely his lifelong habit of asking the right question at the right time, and then driving himself ceaselessly until he could come up with the answers.

For an example of Helmholtz' question-and-answer procedure, I can do no better than to quote his own words as in the translation of Koenigsberger (1906). "In Königsberg I had to teach general pathology and physiology. A teacher in a university is subject to excellent discipline, in that he is obliged each year not only to give at least an outline of the whole of his science, but also to convince and satisfy the clear heads among his hearers, some of whom will be the great men of the next generation. This necessity was most beneficial to myself. In preparing my lectures,

I was led to devise the method of measuring the velocity of the nervous impulse, and also to the conception of the ophthalmoscope. This instrument became the most popular of my scientific achievements; but I have already pointed out to the oculists how much good fortune, rather than any personal merit, favoured me in its invention. I was endeavouring to explain to my pupils the emission of reflected light from the eye, a discovery made by Brucke, who would have invented the ophthalmoscope had he only asked himself how an optical image is formed by the light returning from the eye. In his research it was not necessary to ask it, but had he asked it, he was just the man to answer it as quickly as I did, and to invent the instrument. I turned the problem over and over to ascertain the simplest way in which I could demonstrate the phenomenon to my students. It was also a reminiscence of my days of medical study, that ophthalmologists had great trouble in dealing with certain cases of eye disease, then known as black

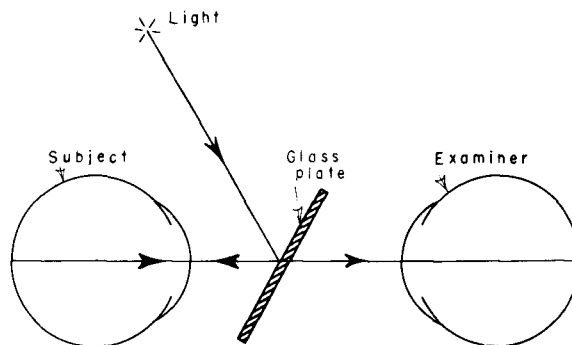


Fig. 3. Principle of the Ophthalmoscope (Ogle, 1961).

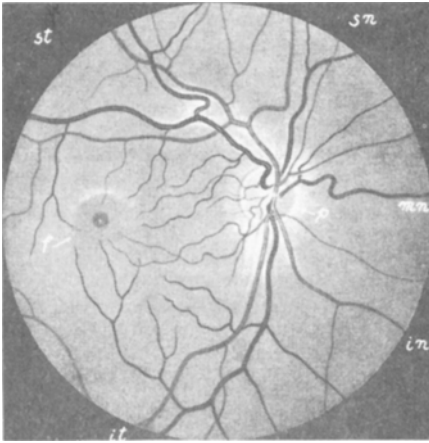


Fig. 4. Ophthalmoscope view of a human retina. (Reprinted from *The vertebrate visual system* by S. Polyak by permission of The University of Chicago Press. Copyright, 1957.)

cataract. The first model was constructed of pasteboard, eye lenses, and cover glasses used in the microscopic work. It was at first so difficult to use, that I doubt if I should have persevered, unless I had felt that it must succeed; but in eight days I had the great joy of being the first who saw before him a living human retina."

Figure 2, taken from a recent paper by Rushton (1962), shows the phenomenon studied by Brucke, namely the reflection of light from the back of the eye of a cat. The solid lines show that this light, focused on the retina and reflected from the tapetum or reflecting surface beyond it, returns from each point on the retina along the same path as the entering rays. Helmholtz' (1851) achievement was basically to provide a partially reflecting surface and a light source, as shown in Fig. 3. This drawing, from a book on optics by Kenneth Ogle (1961) shows that an examiner can direct light into the eye of his subject and then place his own eye in a position to receive the rays returning from the subject's retina through the partially reflecting mirror. If both examiner and subject are focusing the rays correctly, the subject's retina is clearly seen by the examiner as a glowing tissue with all its structures laid bare, as in the fundus view from Polyak (1957) in Fig. 4. Later refinements of the instrument have included a built-in light source, suitable lenses to correct or evaluate the focusing power of the subject's eye, and a camera to photograph the back of the eye, nowadays with Kodachrome or Polaroid color film.

I could spend the remainder of this talk in a mere enumeration of Helmholtz' scientific contributions, starting with his enunciation of the principle of the conservation of energy (1847) and including his measurement of the speed of the nerve impulse (1850), his monumental treatises on physiological optics 1856-1866) and acoustics (1863), and his concept

of unconscious inference as the basis for perception (1855). But if Helmholtz were with us today he would himself be very impatient with any such catalog; instead he would remind us, I am sure, that ~~it~~ has been over a hundred years since he asked some very pertinent questions about color vision, pitch discrimination, and many other scientific problems of his day. He would wish, in short, to have us tell him what we have been able to find out in the years since his time and how his theories *look* to us, now that we have been able to test them against modern experimental evidence. So, for the rest of this talk, let us examine that evidence in one particular segment of knowledge, namely that of the fundamental basis for color vision.

We recall that a trichromatic theory of vision had been suggested by Thomas Young in 1802. The suggestion went unnoticed until Helmholtz revived it fifty years later, after careful experimentation with additive color mixture convinced him of its basic validity. Helmholtz also gave the theory a plausible physiological and psychological foundation by relating it to Müller's doctrine of the specificity of nerve impulses. He drew the three hypothetical receptor sensitivity functions (Helmholtz, 1856-66) shown in Fig. 5, and started a seemingly endless progression of attempts to draw other such curves in such a way that they would give a quantitative description not only of color mixture, but of every other aspect of color vision as well. The trichromatic theory is now familiar to every beginning student under the compound name of the Young-Helmholtz theory. In its simplest form, the theory maintains that three and only three types of receptor are required for the discrimination of hue, despite the fact that there is an infinite hue range corresponding to the continuous distribution of wavelengths available in the spectrum as well as in non-spectral mixtures of light. In accordance with Müller's principles, red is a sensation specifically corresponding to a strong excitation of the receptors of type 1 in the diagram, together with weak excitations

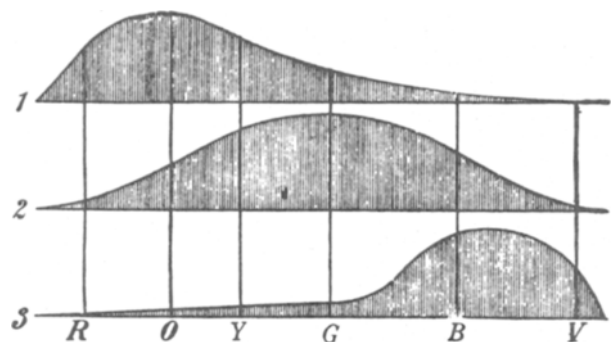


Fig. 5. Sensitivity functions of hypothetical red (1), green (2), and violet (3) receptors (Helmholtz, 1856).

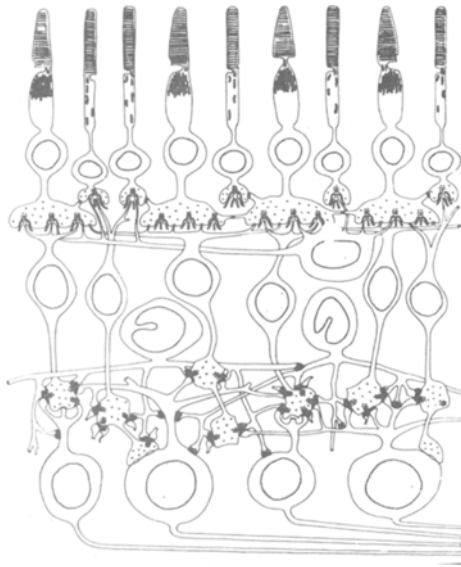


Fig. 6. Diagram of retinal interconnections (Dowling and Boycott, 1966).

of types 2 and 3. All other hues result from varying proportions of stimulation of the three types, and thus the whole range of pure spectral lights and their mixtures can be analyzed by a three-receptor system.

The evidence for the existence of at least three elements has always been overwhelming; a two-element or a one-element system could only result in abnormally poor color discrimination such as is, in fact, found in the eyes of some animals and in severely color-blind persons. It has not been possible, however, to argue convincingly against a four-, five-, or multi-element theory of color vision. The phenomenal purity of yellow, together with facts of color contrast and other considerations of a psychological nature, led Hering and many others to adopt color systems involving four or more primary colors. Furthermore, the later theories substituted dynamic processes of mutual excitation and inhibition among the separate elements for the simple additive action assumed by the Young-Helmholtz theory. The evidence for such processes finally became almost as compelling as the support for the trichromatic theory. Modern investigators of color (e.g., Judd, 1951) were led to "zone" or "stage" theories in which trichromatic receptor activity was assumed to produce, at later stages in the visual process, an opposition between yellow and blue, for example, or between red and green. Physiological evidence has brought new support for such complex theories and has justified the emphasis placed upon them (e.g., by Hurvich & Jameson, 1964) since the time of Hering. The studies of Svaetichin (1956) in the fish retina and of De Valois (1960) in the monkey lateral geniculate body provide particularly striking evidence for the existence of opponent processes.

But what of the trichromatic theory? Are the ideas

of Young and Helmholtz too simple to account for the behavior of photoreceptors? Are there four or more types of receptor rather than three? Does each receptor contain a mixture of several different photopigments? Are there luminosity receptors, as well as receptors specialized for color? Countless psychophysical studies of color vision have failed to provide answers to these simple questions.

This reminds me of a story in the current issue of *Readers Digest*:

"There was a lecture on Long Island recently for a group of housewives. The subject was 'A Happy Sex Life.' At the conclusion there were questions and answers. Finally the lecturer asked, 'Are there any more questions?' From the back of the room came: 'Are there any more answers?'"

Yes, there are answers to the questions about color receptors, thanks to recent work using a variety of experimental techniques. Let us review them at this time as we commemorate Helmholtz' great insights into this subject.

First, let us look at the structures involved. Figure 6 shows simplified diagram by Dowling and Boycott (1966), based on their examination of the primate retina with electron micrographs. The action of light occurs in the outer segments of the rods and cones, the structures at the top of the diagram that contain piles of membrane-limited discs. Somehow the light causes molecular changes within these discs, and signals are then transmitted to the bases of the receptors, where they can be picked up by the nerve fibers that synapse with them in the outer plexiform layer. Notice that multiple connections exist at this early level; Dowling (1965) has reported finding 36 or more synaptic contacts with a single cone of the primate fovea. Horizontal cells supply interconnections among non-adjacent receptor cells, while bipolar cells



Fig. 7. Portion of outer segment of a cone from the fovea of a monkey (Dowling, 1965).

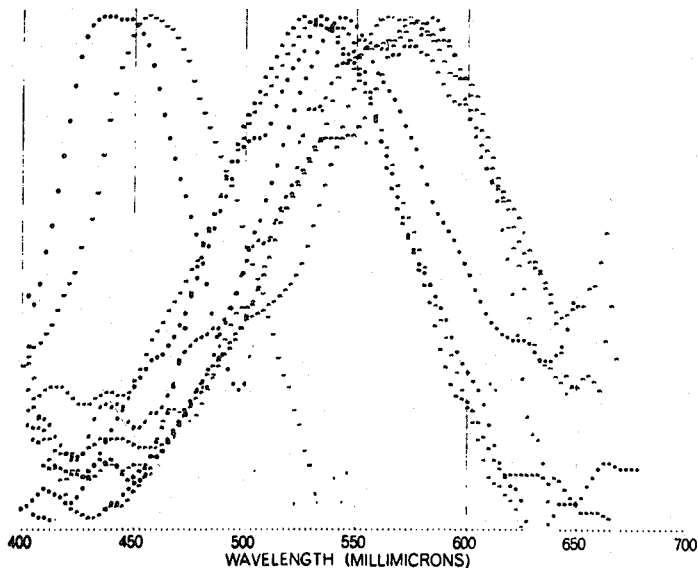


Fig. 8. Differential spectral sensitivity curves for ten separate cone cells (Marks, Dobbie and MacNichol, 1964).

carry the signals to the inner plexiform layer. There again, neural interaction can take place, since amacrine cells communicate with widely separated bipolars in the regions where bipolars synapse with the retinal ganglion cells, near the bottom of the figure.

To understand the retinal basis for color vision we need to start with the cone receptors and ask whether three or more types of them can be identified. Then we need to know how signals from one receptor are enhanced or inhibited by signals from another, and how these modified signals are further processed in the inner plexiform layer. We must clearly realize that any signals carried to the brain along optic nerve fibers are coming not from the receptors, but from the retinal ganglion cells that are the final collectors of information from complex retinal networks. Is it any wonder that there are so many theories of color vision, or that none has been proven or disproven by a hundred years of psychophysical research? What we obviously need, more than anything else in this field, is a detailed knowledge of how each separate part of the system works, starting first of all with the outer segments of the cone receptors. Exciting new technical advances of the past few years have begun to provide that knowledge, from a number of separate lines of research.

Several investigators have now been able to direct a fine beam of light at the tip of one cone receptor at a time. They can then measure the absorption of light of all wavelengths by the particular pigment within that receptor. Other investigators have placed a tiny recording electrode within a single cone receptor cell, and have thus measured the electrical signal generated by each particular cell in response to all different wavelengths of light. These investigations have shown, as we shall see, that three separate types of cone

receptor are indeed present in eyes known to have color vision. It is interesting that even the best electron micrographs of cone outer segments, such as the one by Dowling (1965) have so far failed to reveal structural differences corresponding with the differences in spectral sensitivity (Fig. 7). Still other investigators, working with living human eyes, have obtained much less direct evidence of receptor function but have nevertheless succeeded in getting their information from very early stages in the visual process. In some of this work, measurements are made of the absorption of light by the photopigments in the retina of the living eye. In still other studies, electrical responses are

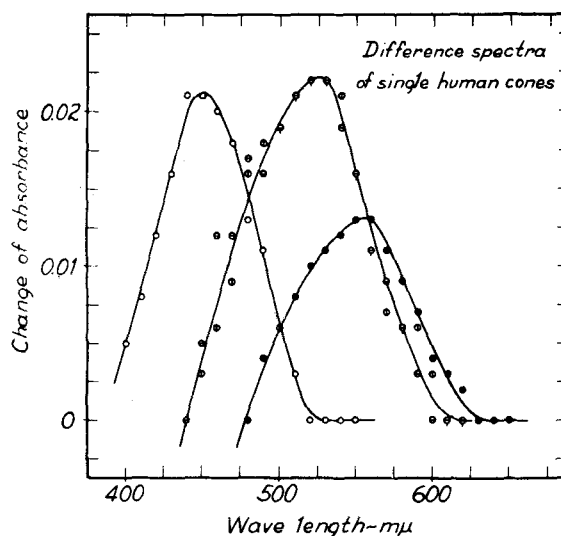


Fig. 9. Difference spectra of four human cones (Brown and Wald, 1964).

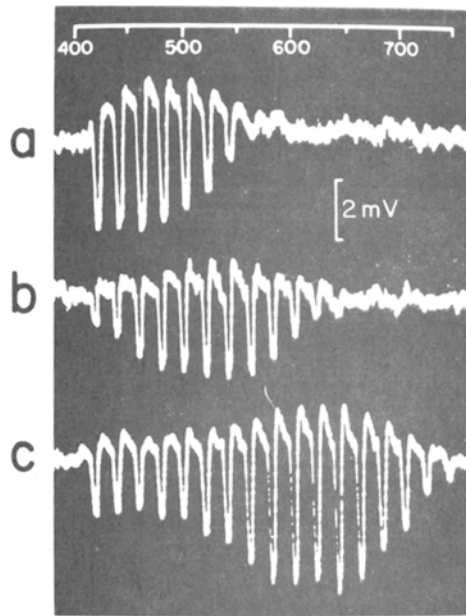


Fig. 10. Response potentials recorded by Tomita et al (1966) from blue- (a), green- (b), and red-sensitive (c) cone cells of the cap.

recorded from the human eye under conditions where the color-discriminating mechanisms are known to generate the response. Let us look briefly at some of the facts uncovered by these diverse lines of research.

Within the last three years two laboratories have reported successful determinations of the light-absorption characteristics of individual monkey and human visual cones. The technique is a difficult one, involving the bleaching of the cone pigment and the careful determination of differences in absorption before and after bleaching. Marks, Dobbelle, and MacNichol (1964) took a small piece of retina and placed it, receptor side up, in a gelatin-saline medium sealed with paraffin. They then used a microscope, together with infra-red image converting devices, to center an extremely fine beam of light on an individual cone receptor. Appropriate analyzing arrangements were then made to record the spectral sensitivity curve of each receptor cell by means of automatic operation of a digital computer. The net result, on 10 separate cells from human or monkey retinas, is shown in Fig. 8. The curves printed out by the computer appear to fall in three major groups, with maximum differential absorption at about 445, 535, and 570  $m\mu$ .

Similar experiments were carried out at about the same time by Brown and Wald (1964). Difference spectra for four human cones are shown in Fig. 9. The authors conclude that they have identified a blue, two green, and a red receptor having maximal absorption at about 450, 525, and 555  $m\mu$ , respectively. These figures are not in complete agreement with those

of Marks, Dobbelle, and MacNichol, and the number of cases is too small to permit any safe generalization as to types of receptor within the whole population of human visual cones. Nevertheless they give convincing proof of the major aspect of the Young-Helmholtz theory, namely that each visual receptor is specialized to absorb light over a limited range of wavelengths, with a maximum absorption at a particular region of the spectrum. It is also clear that very substantial differences exist from one receptor to another; this refutes a color receptor hypothesis such as that of Hecht (1934) who supposed that there were only small differences among the various types of color receptor.

Even more recent is the first bona fide recording of electrical response potentials from single cone receptor cells. Again, the technical difficulties have been very great. They were surmounted by Dr. T. Tomita and associates in Tokyo last year. Tomita tells of watching a pneumatic drill being used to break holes in the hard pavement outside his laboratory one day. The thought occurred to him to use the same principle to drive a fine microelectrode into the hard surface of a single cone receptor. Unfortunately, however, he

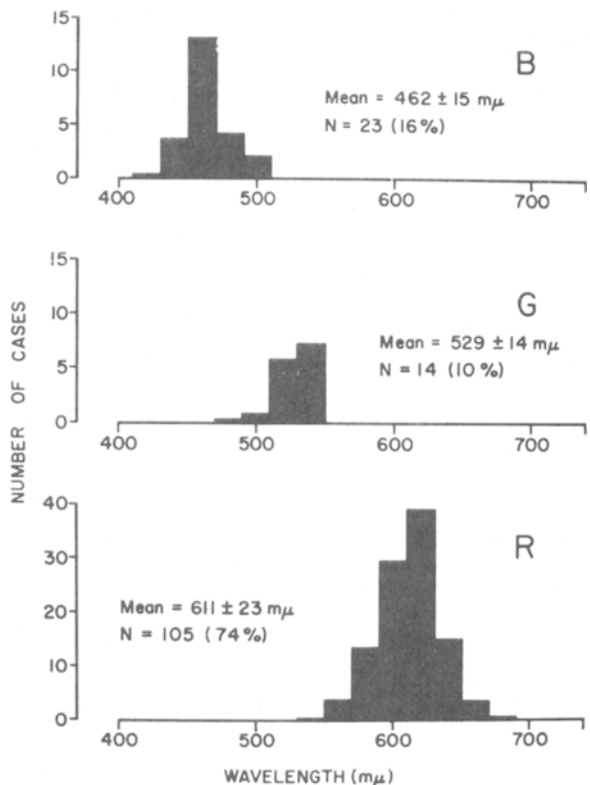


Fig. 11. Histograms of peak wavelengths for 142 cone receptors (Tomita et al, 1966).

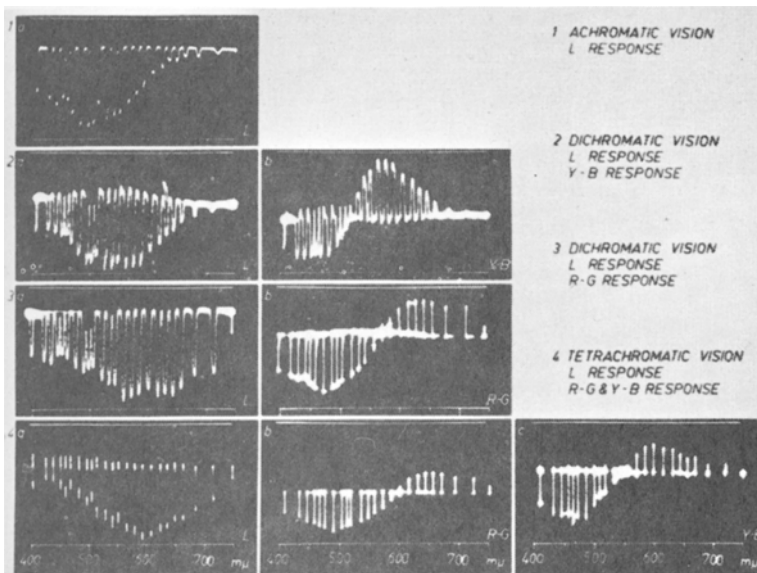


Fig. 12. Response potentials from single cells in a retinal region proximal to the receptors of fish having various forms of color vision (Svaetichin and MacNichol, 1958).

found that the trick did not work on so small a scale. Even with the use of high-frequency, controlled vibration, the electrode invariably whipped around and broke before any successful penetration could be achieved. At this point, however, Tomita asked himself a truly Helmholtzian question: if the electrode cannot be vibrated, why not hold the electrode still and vibrate the retina instead? This is the trick that enabled him to use an ultra-micropipette of very fine dimensions. To be effective, the electrode tip must have a diameter of about one tenth of a micron, so small compared to the wavelength of light that it can never be seen under a light microscope. Only the largest cone receptors can be used; so far the experiments are on the retinas of the carp and other fish known to have color vision.

Figures 10 and 11 represent receptor response potentials from three separate types of cone receptor in the carp. (I am indebted to Dr. Tomita for these figures showing unpublished work of the last few months by him and his associates, Murakami, Kaneko, and Pautler.) The stimulus consists of successive flashes of monochromatic light equal in number of quanta at 20  $m\mu$  intervals throughout the spectrum. It is clear in Figure 10 that blue-, green-, and red-sensitive receptors produce the responses shown in records a, b, and c. Each response is a monophasic, graded potential whose magnitude reflects the spectral sensitivity of the receptor cell. Figure 11 presents frequency distributions of the peak wavelengths for 142 cells whose spectral responses could be determined. It is clear that three groups of cells are found, with a preponderance of red-sensitive ones with peaks in the vicinity of 611  $m\mu$  and lesser numbers of green-sensitive ones at about 529  $m\mu$  and blue-sensitive ones at about 462  $m\mu$ . What better evidence could be found for the validity of the Young-Helmholtz theory

at the level of receptors? It is particularly significant that fish had been used in earlier experiments in which the electrode tip was not in the receptor cells but in the layer of bipolar and horizontal cells. Response potentials recorded in that region were the S-potentials described by Svaetichin (1956) and shown in the records of Fig. 12 (from Svaetichin and MacNichol, 1958). Some of these potentials reverse their polarity as the spectrum is traversed; they provide strong evidence for opponent processes like those demanded by the Hering theory of color vision. Thus we may con-

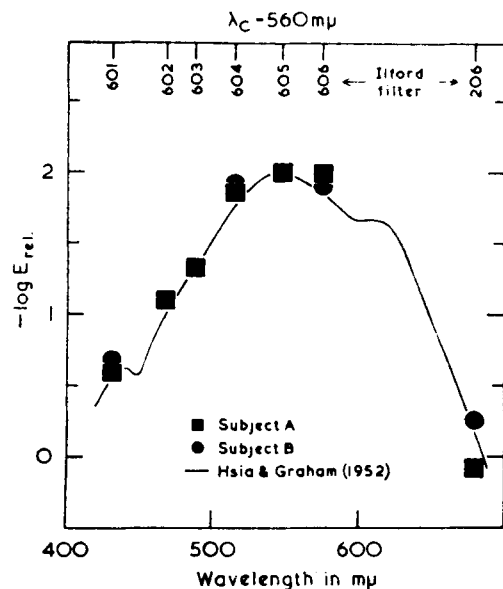


Fig. 13. Effectiveness of lights of various wavelengths for bleaching human cone receptors (Ripps and Weale, 1964).

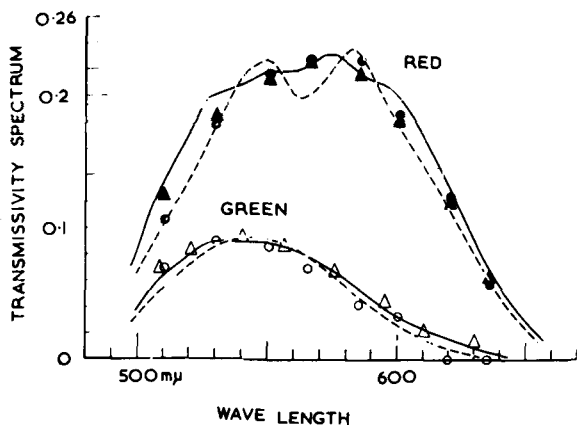


Fig. 14. Bleaching of a red pigment and a green pigment in human cone receptors (Baker and Rushton, 1965).

clude that, at least in the retina of a fish, Helmholtz and Hering rule separate regions that are only a fraction of a millimeter apart.

But what of the responses of our own eyes, or those of other primates? It is unfortunately true that the cone receptors are smaller and more delicate than in the eyes of fish, and the problems of recording from single receptors seem all but insurmountable at the present time. The fish results can serve as a guide, however, in interpreting some less direct evidence that we have on primate receptor activity.

One technique, used by Rushton and Campbell, and by Weale and others has been to shine light into the human eye and measure the light reflected back out again through the retina, the same basic procedure as the one used by Helmholtz for the ophthalmoscope. The entering beam of light passes through the retina, is reflected by the layer in back, and returns along the same path back out through the retina again. This means that the more dense the retinal pigments, the less light will be reflected back out of the eye. Now there are many pigments in the eye, but the ones in which we have a particular interest are the photopigments lying within the visual receptors, rods and cones. Exposure to a strong light causes these pigments to be bleached; that is, their optical density is reduced. Hence the receptor pigments can be studied by a difference method, one in which the light reflected through the retina is measured twice, once before bleaching and once after bleaching by a strong light.

Figure 13 shows some results on two subjects as obtained by Ripps and Weale (1963). It shows, on the ordinate scale, the relative energy of light required to cause a given amount of change in retinal density. The lights used for the bleaching were those provided by color filters as indicated throughout the visible spectrum. Measurements are for the fovea, where only cone receptors are present. The plotted data show

good agreement with the curved line representing psychophysical threshold determinations of spectral sensitivity of the foveal region by Hsia and Graham (1952). These results support the conclusion that events at the very beginning of the visual process, namely the bleaching of the cone pigments, are highly correlated with what might be called the end result, namely the subjectively determined visual sensitivity thresholds.

Experiments recently reported by Baker and Rushton (1965) have been concerned not with the overall bleaching of the retinal cones, but with a green pigment and a red pigment isolated by the use of color-blind subjects and by selective bleaching procedures. Again the results of retinal densitometry measurements, as shown by the plotted points in Fig. 14, are in substantial agreement with the corresponding psychophysical functions obtained by Hsia and Graham (1957) and by Stiles (1959). Thus the action of light on two of the three pigments demanded by the Young-Helmholtz theory has been measured in the human eye. The third type of cone, the blue-sensitive one has not yet been identified by the reflection densitometry procedure. This is probably because of technical problems associated with the use of shorter wavelengths of light. Taken together, all these studies appear to confirm the adequacy of the Young-Helmholtz trichromatic theory to deal not only with events at the receptor level but with psychophysically determined spectral sensitivity functions.



Fig. 15. Subject wearing a contact lens electrode and a reference electrode taped to the forehead (see Riggs, 1963).



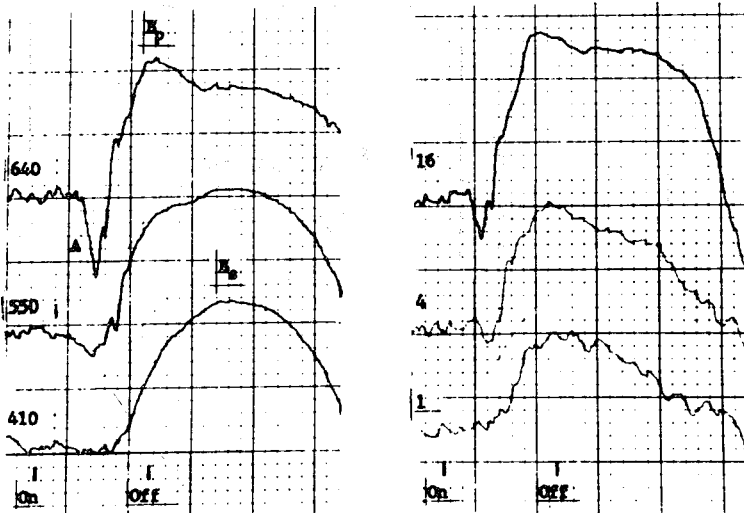


Fig. 16. Typical human electroretinograms showing components ( $A$ ,  $B_p$ ) triggered by cones and ( $B_s$ ) by rods (see Cogan, 1966).

The last example I wish to present of new human data in conformity with the Young-Helmholtz theory is taken from work in our own laboratory at Brown University. We have worked out a technique for recording electrical responses from the human retina under conditions in which we believe we have confined the responses to those initiated by stimulation of the cone receptors. To do this we have started with conventional procedures for recording the human electroretinogram and have introduced new technical refinements to isolate the color-specific responses in which we are most interested.

Figure 15 shows a subject wearing a contact lens electrode, together with reference electrodes that permit the recording of responses generated in the eye upon stimulation by light. During the last 25 years a large body of information has been gathered about such responses in their dependence upon the intensity, wavelength and other characteristics of the stimulating light as well as the state of the eye with regard to adaptation, clinical condition, etc. (see Riggs, 1965). We now know that the electroretinogram is not directly generated by the receptors, but arises mainly from neural cells in immediate contact with them. Figure 16 shows typical responses of a normal eye to stimulation by 0.1 sec. flashes of light (see Cogan, 1966). The three records on the left illustrate differences in waveform due to changes in wavelength of stimulation. For the top record the stimulus wavelength was set at  $640\text{ m}\mu$ , which strongly stimulated cone receptors; these receptors triggered their associated neurones to produce a negative A-wave and a positive B-wave,  $B_p$ . For the bottom record the wavelength was set at  $410\text{ m}\mu$ , which caused such a large rod-initiated response,  $B_s$ , that scarcely any cone-initiated response can be seen. In the middle record, at  $550\text{ m}\mu$ , the cone-initiated A- and  $B_p$ -waves are present along with a large rod-initiated  $B_s$ -wave. The series of records

on the right shows that cone responses are prominent at high stimulus intensities, while low intensities evoke mainly rod responses. It is clear from these records that no satisfactory use can be made of electroretinographic techniques for the study of color vision until the large signals triggered by the rod receptors can somehow be eliminated. This has only recently been accomplished by the use of an average response computer and a novel form of stimulus presentation (Riggs, Johnson, & Schick, 1964). The stimulus field is shown in Fig. 17. The subject fixates steadily on the point at the center of the field. The stimulus pattern is a set of stripes that alternate with one another; a stripes can be green, for example, and the b stripes red. While the subject is fixating, the wavelengths are quickly interchanged, so that the a stripes become red and the b stripes become green. This interchange continues to be made at the rate of 10 changes

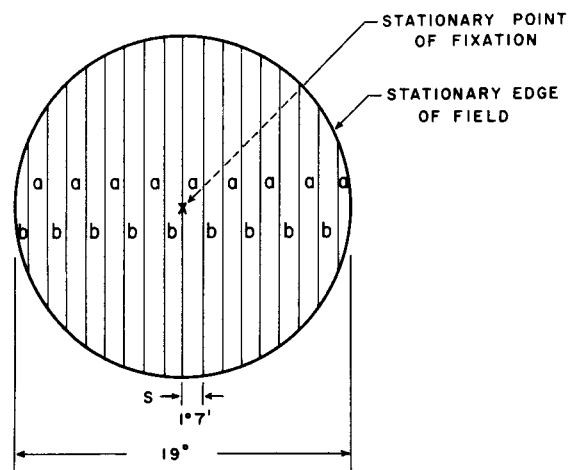


Fig. 17. Stimulus field of alternating stripes (Riggs, Johnson, and Schick, 1966).

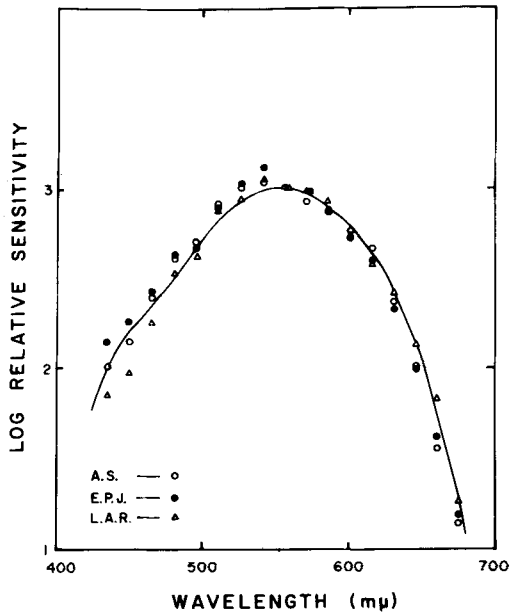


Fig. 18. Brightness matching data on spectral sensitivity for three subjects (Johnson, Riggs, and Schick, 1966).

per second. The result is that, within the retinal image of this pattern, each cone receptor is alternately exposed to red and green lights. Thus each receptor can be assumed to trigger a response wave that is dependent upon the differential sensitivity of that receptor to red and green lights. Thus we record a train of response potential waves, each of which is elicited by the alternation of wavelength in the stripes of the stimulus pattern.

A basic set of experiments (Johnson, Riggs, & Schick, 1966) has established the photopic nature of responses obtained in this way. Figure 18 shows psychophysical data obtained for the three of us by a brightness matching technique. The curve is the extra-foveal cone sensitivity function of Wald (1945), with which our data appear to be in reasonably good agreement. Figure 19 shows points plotted from electrical data for sensitivity to wavelengths taken in steps of 15 mμ throughout the visible spectrum on the same three subjects. While the variability is necessarily large with the very small signals we used for our criterion amplitude measures, the overall picture is one of conformity to a psychophysical cone sensitivity function. Figure 20 shows, for one subject, the agreement between three separate electrical determinations (shown by the data points) and his own psychophysical function (solid line curve). This agreement, together with certain control experiments, has led us to conclude that the responses we obtain are triggered by cone receptors, rather than by rods.

On the basis of the above experiments it was possible to designate, for each one of us, the energy

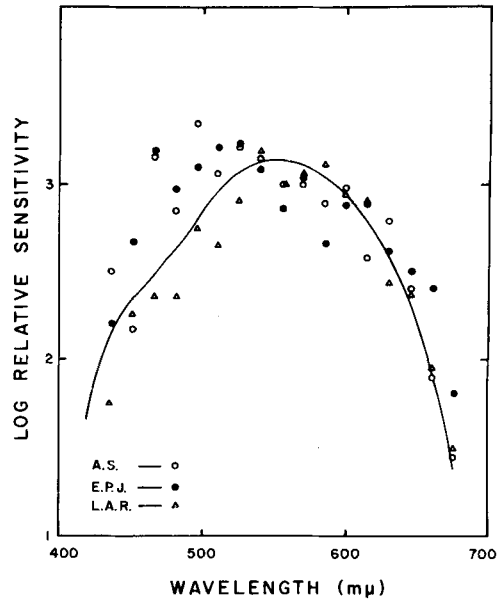


Fig. 19. Electrical response data on spectral sensitivity for three subjects (Johnson, Riggs, and Schick, 1966).

of light at each point on the spectrum that would yield the same size of electrical response. We then conducted a series of experiments in which the alternate stripes in the stimulus field were of two different wavelengths but of equal stimulating ability (Riggs, Johnson, & Schick, 1966), as in Fig. 21. Sample records obtained when the colors were alternated are shown in Fig. 22.

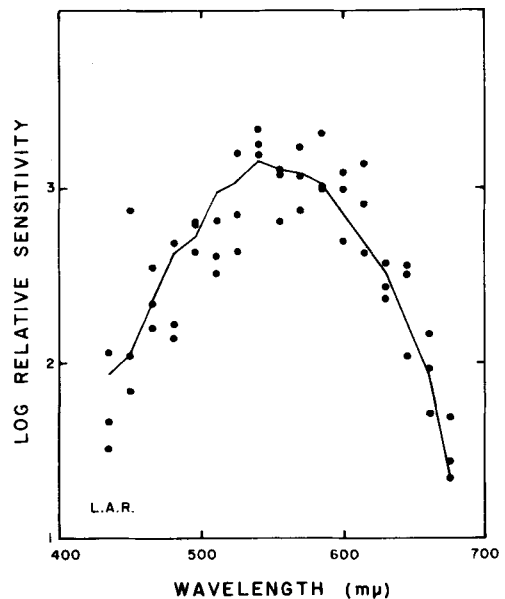


Fig. 20. Brightness matching data (curve) and electrical data (points) for three experiments on the same subject (Johnson, Riggs, and Schick, 1966).

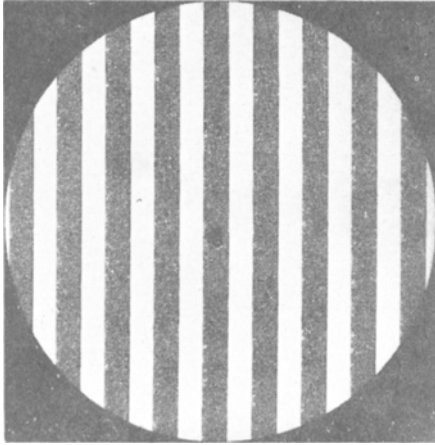


Fig. 21. Alternate stripes of two different wavelengths (original in color).

These are half-second portions of records showing five response potential waves generated by alternations of wavelength in the stimulus stripe pattern. In this series of records, one of the wavelengths is maintained at  $675\text{ m}\mu$ . This wavelength was alternated with another wavelength specified by the number beside each record. It is clear that alternation between  $675\text{ m}\mu$  and  $435\text{ m}\mu$ , in the record at the top produces relatively large potential waves, while very small responses are recorded when  $675\text{ m}\mu$  is alternated with  $645$  or  $660\text{ m}\mu$ , as in the records near the bottom. The step record below the others is a calibration showing a  $1\text{ }\mu\text{V}$  display produced by a photocell responding to one set of stripes. It is clear that the eye responds to alternations in wavelength even when the stripe intensities are adjusted to equivalent values. Hence we are dealing with wavelength-specific responses rather than responses to stimulus intensity.

A more complete display of the results for one subject is shown in Fig. 23. This pictorial matrix illustrates the fact that each of 17 wavelengths symbolized by the horizontal strips is paired with each other wavelength symbolized by the vertical rectangles, to produce an electrical response. The height of each vertical rectangle, moreover, has been made proportional to the magnitude of response resulting from alternation between the corresponding two colors. It is again clear that large responses occur only in response to large wavelength differences. An opponent-color hypothesis might predict particularly large responses from a red-green pair or a blue-yellow pair. This does not appear to be true; the largest responses are found with red-blue pairs, and in fact no wavelength can be found which yields large responses when paired with yellow. We spent a long time making this chart with bits of colored paper, and I now have it hanging in my office. When my wife first saw it there she asked, "Who's your decorator?"

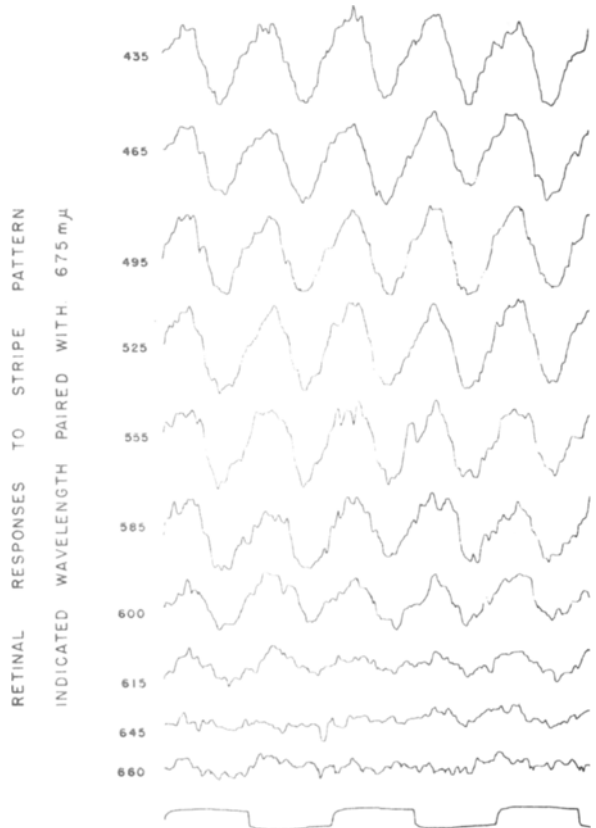


Fig. 22. Sample records of responses of the human eye to alternation between two wavelengths of light (Riggs, Johnson, and Schick, 1966).

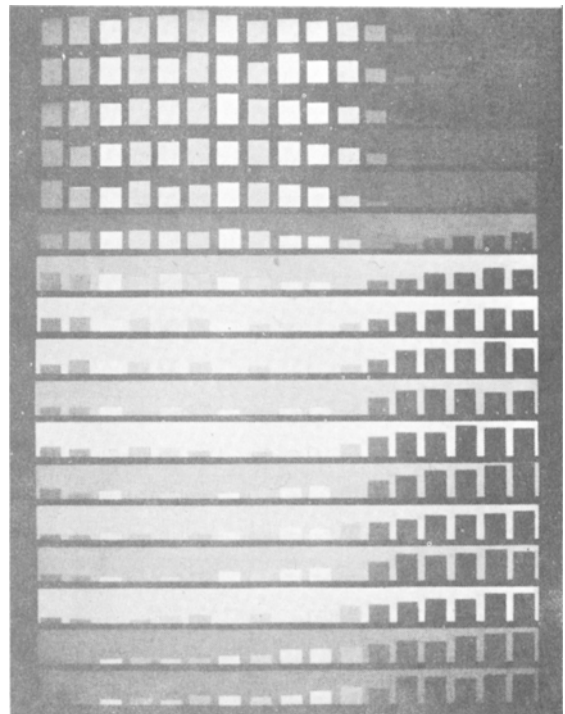


Fig. 23. Pictorial display of magnitudes of response to wavelength alternation in one subject (original in color).

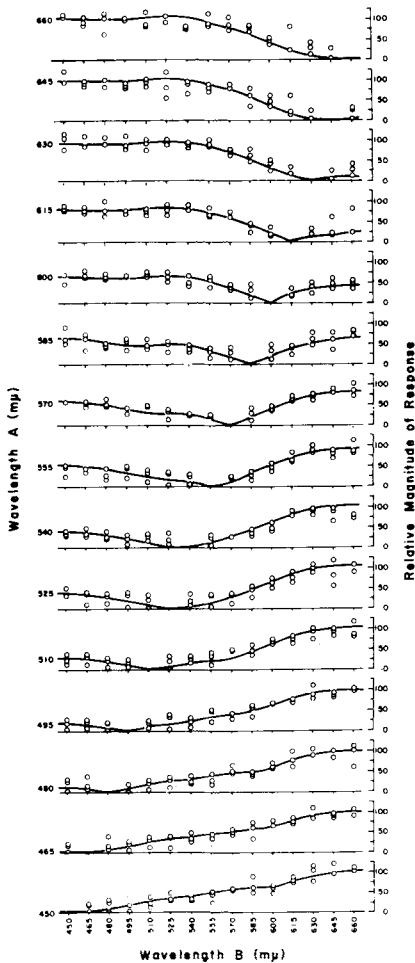


Fig. 24. Magnitudes of response for three subjects (data points) with alternation between wavelengths A and B (Riggs, Johnson, and Schick, 1966).

Figure 24 shows plotted points indicating measured amplitudes of response for all three subjects. The lines drawn through the points indicate an attempt at curve-fitting based on a simple, additive trichromatic hypothesis. In arriving at these lines we have used the coefficient curves shown in Fig. 25 for three possible color elements, R, G, and B. We assume, with Helmholtz, that light at the long-wave end of the spectrum arouses only the R-mechanism, and that there is a broad G mechanism with a peak at 540  $m\mu$  and a B mechanism that functions chiefly at the shorter wavelengths. We remember that all the stimuli used in the experiment have been adjusted to produce comparable sizes of response. Hence we assume that the response we obtain by alternating between wavelengths is made up of the sum of the contributions of these three mechanisms. As an example, we take alternation between 660 and 450  $m\mu$ . The R contribution to the response is 50 units, since it does not respond at all to 450  $m\mu$  and responds by 50 units to 660  $m\mu$ . The G contribu-

tion is similarly found to be 17 units, and the B contribution is 34 units. The sum, 101 units, is the relative height of response for the point on the fitted curve in the preceding figure. In fact, the exact shapes of the three coefficient curves have been arrived at by methods of approximation that yield a reasonably good fit to the data, as shown in the previous figure.

Finally, we may lay out the wavelengths used in this experiment in such a way as to produce a sort of chromaticity diagram, as in Fig. 26. Here the distance between any two wavelengths is approximately proportional to the electrical response potential of the eye when alternating between them. For example, the dashed line has a length of 101 units, as already found for the case of pairing 660  $m\mu$  with 450  $m\mu$ . This figure shows that at least three dimensions are required to express the data. A two-dimensional system would have all the wavelength points falling along a straight line. A four-dimensional diagram, taking us out of the plane shown here, is not found to be necessary to achieve a good fit to the data. We conclude that, for the early stage in the human visual process from which the electroretinogram waves are coming, a formulation of the Young-Helmholtz type is justified. There is as yet no need to assume the existence of a yellow receptor or of opponent processes taking place between complementary pairs. We assume that such processes begin only at higher levels of the visual system.

Helmholtz died in 1894, at the age of 73. Suppose he could have kept on living instead, and could even now be continuing to pursue his scientific career. Just what would he be doing at the present time? Would he join the large group of laboratory researchers who make out grant applications each year so that he and his staff could purchase the necessary monochromators, computers and micro-electrode pullers for the continuance of their work on visual receptors? Would he be a shaper of policy, presiding over the meetings

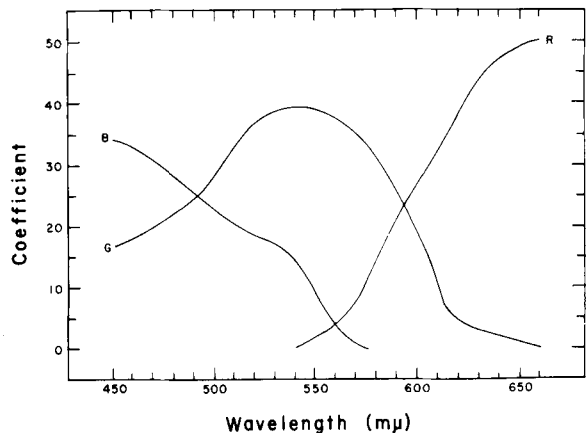


Fig. 25. Coefficient curves for R, G, B color elements (Riggs, Johnson, and Schick, 1966).

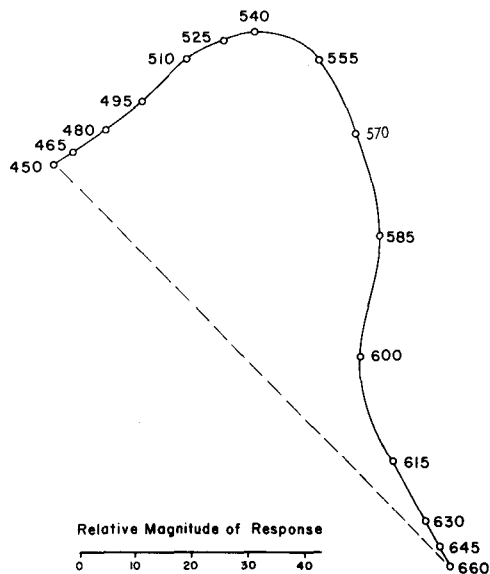


Fig. 26. Diagram showing distances from one wavelength to another as determined by magnitude of electrical response to alteration of wavelength (Riggs, Johnson, and Schick, 1966).

of the national science advisory board? Would he be engaged in the twenty-third edition of his *Physiological Optics* or the nineteenth edition of his work *On the Sensations of Tone*? Perhaps; but I like to think that his time could be saved for the thing that he did best during his natural life-time, namely, looking into some new project of current fundamental interest. Perhaps now it would be in the field of organic evolution, looking for a key to the origin of living macromolecules. Perhaps it would be to find the basis for growth of malignant tissue. Perhaps it would even be closer to our own area of experimental psychology, and lead to an understanding of the molecular basis of learning. Whatever the field of his interest, I am confident that Helmholtz would spend most of his time in looking: looking for facts, looking for the right questions to ask, and only last of all, looking for the answers.

## References

- Baker, H. D., & Rushton, W. A. H. The red-sensitive pigment in normal cones. *J. Physiol.*, 1965, 176, 56-72.
- Boring, E. G. *A history of experimental psychology*. (2nd ed.) New York: Appleton-Century-Crofts, 1950.
- Brown, P. K., & Wald, G. Visual pigments in single rods and cones of the human retina. *Science*, 1964, 144, 45-51.
- Cogan, D. G. *Neurology of the visual system*. Springfield, Ill.: Thomas, 1966.
- De Valois, R. L. Color vision mechanisms in the monkey. *J. gen. Physiol.*, 1960, 43, 115-128.
- Dowling, J. E. Foveal receptors of the monkey retina: fine structure. *Science*, 1965, 147, 57-59.
- Dowling, J. E., & Boycott, B. B. Organization of the primate retina: electron microscopy. *Proc. Roy. Soc. (London)*, 1966, 166, 80-111.
- Hall, G. S. *Founders of modern psychology*. 1912.
- Hecht, S. Vision: II. The nature of the photoreceptor process. In C. Murchison (Ed.), *Handbook of general experimental psychology*. Worcester, Mass.: Clark University Press, 1934.
- Helmholtz, H. L. von. *Über die Erhaltung der Kraft*, 1847.
- Helmholtz, H. L. von. On the methods of measuring very small intervals of time, and their application to physiological purposes. *Phil. Mag.*, 1850, 6.
- Helmholtz, H. L. von. *Description of an ophthalmoscope for the investigation of the retina in the living eye*. Berlin: Förster, 1851.
- Helmholtz, H. L. von. *Über das Sehen des Menschen*, 1855.
- Helmholtz, H. L. von. *Handbuch der physiologischen Optik*, 1866. Eng. trans. 1924, reprinted New York: Dover, 1962.
- Helmholtz, H. L. von. *Die Lehre von den Tonempfindungen*, 1863.
- Hsia, Y., & Graham, C. H. Spectral sensitivity of the cones in the dark-adapted human eye. *Proc. Nat. Acad. Sci.*, 1952, 38, 80-85.
- Hsia, Y., & Graham, C. H. Spectral luminosity curves for protanopic, deuteranopic and normal subjects. *Proc. Nat. Acad. Sci.*, 1957, 43, 1011-1019.
- Hurvich, L. M., & Jameson, D. Introduction and translation of Hering, E.: *Outlines of a theory of the light sense* (orig. 1905-1911) Cambridge, Mass.: Harvard, 1964.
- Johnson, E. P., Riggs, L. A., & Schick, A. M. L. Photopic retinal potentials evoked by phase alternation of a barred pattern. *Vision Res.*, 1966, Suppl. 1, *Clinical Electroretinography*, 75-91.
- Judd, D. B. Basic correlates of the visual stimulus. In S. S. Stevens (Ed.), *Handbook of experimental psychology*. New York: Wiley, 1951.
- Koenigsberger, L. *Hermann von Helmholtz*, trans. by Frances A. Welby. Oxford: Clarendon Press, 1906. Reprinted by Dover Publications, Inc.: New York, 1965.
- Marks, W. B., Dobbelle, W. H., & MacNichol, E. F., Jr. Visual pigments of single primate cones. *Science*, 1964, 143, 1181-1183.
- McKendrick, J. G. *Hermann Ludwig von Helmholtz*, 1899.
- Müller, J. *Handbuch der Physiologie*, 1838.
- Ogle, K. N. *Optics*. Springfield, Ill.: Thomas, 1961.
- Polyak, S. *The vertebrate visual system*. Chicago, 1957.
- Riggs, L. A. Electrophysiology of vision. In C. H. Graham (Ed.), *Vision and visual perception*. Chap. 5. New York: Wiley, 1965.
- Riggs, L. A., Johnson, E. P., & Schick, A. M. L. Electrical responses of the human eye to moving stimulus patterns. *Science*, 1964, 144, 567.
- Riggs, L. A., Johnson, E. P., & Schick, A. M. L. Electrical responses of the human eye to changes in wavelength of the stimulating light. *J. Opt. Soc. Amer.*, 1966, 56, 1621-1627.
- Ripps, H., & Weale, R. A. Cone pigments in the normal human fovea. *Vision Res.*, 1963, 3, 531-543.
- Rushton, W. A. H. *Visual pigments in man*. Springfield, Ill.: Thomas, 1962.
- Stiles, W. S. Colour vision: the approach through increment threshold sensitivity. *Proc. Nat. Acad. Sci.*, 1959, 45, 100-114.
- Svaetichin, G. *Acta Physiol. Scand.*, 1956, 39, Suppl. 134.
- Svaetichin, G., & MacNichol, E. F., Jr. Retinal mechanisms for chromatic and achromatic vision. *Ann. N. Y. Acad. Sci.*, 1958, 74, 385-404.
- Tomita, T., Murakami, M., Kaneko, A., & Pautier, E. L. (Personal communication.)
- Wald, G. Human vision and the spectrum. *Science*, 1945, 101, 653-658.

## Note

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