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STUDIES IN THE THEORY OF VISUAL RESPONSE.

An Attempt to Reconstruct Current Hypotheses of the Neural Mechanism Underlying Visual Sensation by the Use of Modern Physical, Chemical and Biological Conceptions.

Thesis for the Degree of Bachelor of Science.

by

Leonard Thompson Troland...

The Department of Biology and Public Health, Massachusetts Institute of Technology,

May - 1912.
FOREWORD.

The contents of this thesis may be grouped under three general heads: (1) general discussion of the problems and points of view involved in visual physiology, (2) a somewhat cursory review and criticism of current hypotheses concerning the neural mechanism of vision, and (3) a systematic attempt to develop a more or less original hypothesis by the use of definite and quantitative chemical, physical and biological conceptions. Of these three aspects of the work the writer considers the last the most significant, and therefore indicates below the sequence of pages upon which it is most apparent.

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May 20, 1912.
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ZQ. Vision, General, 475-477
ZA. Subjective Visual Phenomena, General, 478
ZS. Subjective Color Phenomena and Relationships, 479
ABBREVIATIONS.........

...J.Q. = Quain's Elements of Anatomy; edited by E. A. Schafer, J. Symington, and T. H. Bryce; vol. 3, part 2; (1909); London.

STUDIES IN THE THEORY OF VISUAL RESPONSE.

Thesis.

PART ONE: THE DEVELOPMENT OF A THEORY OF VISUAL RESPONSE.


Physiological Opticians Amongst the Greeks...... The process of seeing has always excited the curiosity of the philosophic mind. As far back as the fifth century before Christ we find Leucippus (490 - ? B.C.) and Empedocles (490-430 B.C.) and, following them, Democritus (460 - ? B.C.) and Diogenes of Apollonius (460 - ? B.C.) speculating concerning the mechanism of vision. The modern scientific theory of visual sensation, as we shall shortly have occasion to point out, is divisible into two departments, those of fact and hypothesis. Needless to say, the thoughts of the early Greek philosophers with reference to vision were entirely hypothetical. According to Empedocles, visual perception must be ascribed to the collision of particles emitted by external objects with similar particles emitted by the eye; the philosopher conceived the ocular radiations to be of several sorts, taking origin in the

1 GOMPERZ, T.: Greek Thinkers, Eng. trans., L. Magnus; (1905); p. 235.
eyes of different animals. As the author of the hypothesis postulates attraction only of like elements, the division of animal species into those capable of vision at night and those incapable, may be explained by assuming dark particles to be emitted from the eyes of the first, while the occular mechanism of the second can produce only light particles. Thus in the dawn of Greek philosophy we find foreshadowed the method of explanation--and even the exact hypothesis--which it seems necessary to-day to employ in the systematization of the facts of vision. Empedocles also propounded a doctrine of primary and mixed colors. Diogenes of Apollonius believed that objects produce an impression upon the pupil of

Diogenes and Democritus on Vision

the eye through the medium of the air, and being well acquainted with the fact that sight depends upon the integrity of

the optic nerve, he regarded this latter as a vein, by which the pneumatic impress passes to the centers. Democritus, in connection with his doctrine of the atomic cosmos, gave a somewhat more detailed account of the means whereby the mind perceives the external world, although he agreed with Diogenes concerning essentials. Every physical object is constantly shedding tenuous atomic replicas of itself which impinge upon the surface of the eye and there stamp the likeness of their progenitors; the air was necessarily conceived to be involved in this process, but when objects are far away from the eye their long journey through the atmosphere supposedly causes the images to lose size or to become misty and distorted. The great atom-

1st did not stop, however, with a purely physical hypothesis of vision; he set an example for future physiologists by entering the domain of psychology and propounding a theory of primary and mixed colors, modified, indeed, from the earlier teachings of Empedocles. The primaries of Empedocles were white, black, red and yellow; Democritus, foreshadowing the views of Young and Helmholtz, looked upon yellow as a mixed color and substituted red in its place. With the exception of Epicurus (342-270 B.C.) and Aristotle (334-322 B.C.) the later Greek thinkers paid very little attention to the problem of the physiology of vision, for the reign of natural philosophy in Greece was soon cut short by the dominance of idealistic and ethical view-points. Epicurus simply restates the doctrines of his master Democritus. Aristotle, in his encyclopedic way, treats of the visual process. He discards the image hypothesis of Democritus in order to advance the idea that light—or the physical agent in seeing—is an activity of an omnipresent medium which he calls the pellucid. Aristotle also considers the subject of color in De coloribus. The followers of Plato, in general, accepted the Democritian hypothesis.

Post-Grecian Students of Vision up to the Renaissance

In the fourth book of his De Rerum Natura, Lucretius discusses the Democritian doctrine of images, and with regard to this, as in most other points, argues for the views of his master in philosophy, Epicurus. Apparently unacquainted with the writings of Aristotle upon vision, Alhazen (d. 1023) of Basra, the Arabian physicist and mathematician, taught as a new doctrine—in the eighteenth century—that objects are not seen

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by virtue of an emanation from the eye, but that light comes from the object itself and enters the eye. Alhazen, being a successful student of physical optics, being acquainted with the phenomenon of refraction and the action of convex lenses, was able to conjecture the function of the retina, and to deal with the dioptrics of the eye. His work on optics was translated into Latin by Vitelo, a Polish philosopher, in 1270, and printed, together with an original treatise by the translator, in 1572.

The Study of Vision Following the Renaissance

The publication of Vitelo's work and translation was the occasion of further discussion of the subject of vision. Leonardo da Vinci had, in his Trattato della pittura (1519) made some comments upon color perception, and in 1575 a volume was published by Maurolycus of Messina, containing a discussion of the optical relations of the parts of the eye, and in 1593, Giambattista della Porta of Naples, wrote concerning the principles of binocular vision in a treatise, De Refractions. The demonstration by Sir Isaac Newton, in 1672, of the chromatic complexity of white light aroused new interest in the problems of sight. The color triangle, a method of exhibiting the relations existing between the different colors of the spectrum, was invented by Newton himself in connection with his studies in color mixture. He employed in these investigations the method of rotating disks, a device for mixing lights which dates back to the Alexandrians.¹ A treatise, De Visu, by F. A. Jan and W. Kuffner appeared in 1669, just previously to Newton's discovery, and as early as 1670, Robert Boyle had

¹ It is mentioned by Ptolemy in the "Optics."
published certain "Experiments and Considerations Touching Color." The modern school of philosophers also began to interest itself in the matter of sight. Thus, in 1709 George Berkeley published a *New Theory of Vision*, as the basis of his refutation of materialism. A *Compleat System of Opticks*, edited by Robert Smith in 1738 summarized the progress of the science up to that time. J. H. Lambert in 1760 devised a method of mixing lights by combined reflection and refraction, and in 1772 described a color-pyramid, an improvement upon Newton's color triangle, and an ancestor of our modern construction. At about the same time P. van Musschenbroek perfected the rotating disk with colored sectors as a means of mixing specific lights. The history of optics up to the last part of the eighteenth century is given by J. Priestley in his *History and Present State of Discoveries Relating to Vision, Light and Colors* (1772). The discovery, in 1798, by Sommerring, of the human fovea centralis deserves mention at this point.

The Greek philosophers failed to distinguish clearly between visual perception and its immediate cause, and a similar confusion between the objective and subjective aspects of the optical process persists even in scientific circles to the present day. But every advance in the study of visual phenomena is a step away from the naive point of view which makes the color of an object the cause of the color sensation. The progress of physical optics carries us in the same direction. The development of the wave theory of light, suggested by Descartes, and worked

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1 LAMBERT, J. H.; *Photometria, sive de mensura et gradibus luminis, colorum et umbrae*, 1760, p. 527.
2 LAMBERT, J. H.; Beschreibung einer Farbenpyramide, Berlin 1772.
3 MUSSCHENBROEK, P. van; *Introductio ad philosophiam*, 1768, 11,
out in detail by Huyghens in his *Traité de lumiere* (1690), was
retarded by the popularity of the Newtonian corpuscular theory,
so that our modern view of the nature of luminous radiations
was not established until the beginning of the nineteenth cen-
tury. Newton himself distinguished definitely between the sen-
sation and the light which caused it, but his corpuscular hypo-
thesis contained within it the germs of the confusion between
perception and objective process which existed in the old Demo-
critian molecular theory of vision. The final disproof of the
Newtonian view was due to the efforts of Augustin Fresnel (1788-
1827) and Thomas Young (1773-1829), and it marked an important
change of attitude in physiological as well as physical optics.
Sensation could no longer be explained in terms of floating
images. The modern epoch in physical optics began, however, with
Maxwell, in 1873, when he showed the light is without doubt
an electro-magnetic phenomenon. Any theory of the visual pro-
cess which pretends to be conclusive must take into considera-
tion the elementary conceptions, at least, of Maxwell's theory.

The remarkable advances made in the
Physiological 
*Optics in the* 19th Century...
knowledge of the physics of light during the first part of the nineteenth century
led to a quickened interest in the problem of its relation with physiological and psychological response. It was not until the middle of the century, with the publication of Helmholtz's great treatise that research in this department of science assumed the enormous proportions manifest at the close of the most re-
markable hundred years of human progress that the world has yet experienced. It will be impossible to even mention here all

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1 Maxwell, J. C.: Electricity and Magnetism, 1873.
of the valuable contributions which have been made to our knowledge of the mechanism and of the general phenomena of vision during that century; only the most important studies will be given historical consideration.

The Rise of the Three-Color Hypothesis......

In this thesis we are concerned primarily with those facts and conceptions which have a bearing upon the purely neural aspect of the visual process. For that reason we shall neglect the advances in the subject of the dioptrics of the eye, which were made in the nineteenth century. The most significant event in the progress of the science of visual sensitivity during the modern period was undoubtably the invention by Thomas Young, of the so-called three-color theory of visual sensation. This hypothesis was first propounded in a paper, On the Theory of Light and Colors, read before the Royal Society on November 12, 1801. In this paper Young selected red, green and blue as primary colors, thus coming into conflict with the currently accepted teachings of David Brewster—who regarded red, yellow, and blue as primary—and asserted, moreover, that these fundamental sensations were to be referred to the action of three specific elements in the retina, which responded selectively to lights of different wavelengths. In a popular restatement of his doctrine, in his Lectures on Natural Philosophy, 1807, Young changed the primaries to red, green and violet, a choice in which he was probably guided by the extreme nature of the positions of these colors in the spectrum, and in which he had been forestalled by Wunsche, an earlier thinker. As in many other of his views,

1 Versuche und Beobachtungen über die Farben des Lichtes, Leipz.
however, Young here proved himself to be greatly in advance of his times; his hypothesis was given little attention, or was misinterpreted, by his contemporaries. Credit for the revival of the three-color hypothesis is usually given to Hermann von Helmholtz, who employed it as an explanatory agent in connection with his monumental work upon the subject of physiological optics which appeared in 1860. But it seems that the praise is actually due to Maxwell, for Helmholtz had discussed Young's hypothesis in 1852, only to discard it, and only after becoming acquainted with the researches of Maxwell, made in 1856 and 1857, upon the subject of color mixture and in which the three color hypothesis received special mention and support, did he finally adopt it. Another claimant of the honor is J. P. Durand, a French physiologist who published on the subject in 1855. In the hands of Helmholtz the three-color hypothesis became what Young never held it to be, -- a three-nerve-fiber hypothesis. Following the researches of Holmgren, Hering, and Isaachsen upon the space limen for colors, however, Helmholtz relinquished the idea that the selective elements of the retina were individual nerve terminations, and the three-color hypothesis, originally mechanical in its implications, began to fall in line with the developing ideas of the chemistry of the visual process. With the death of Helmholtz in 1894 the three-component hypothesis--as it is best called--was left in the care of certain of his pupils, Arthur Konig, professor of physics at Berlin, Johannes von Kries, professor of physiology in the University of Freiburg im Breisgau, having been most prominent

1 HELMHOLTZ, H. v.: Ueber die Theorie der zusammengesetzten Farben; Müller's Arch. f. Anat. u. Physiol., 1862, pp. 461 f. (over)

3 DURAND (DE GROS), J. P.: Les Origines de la theorie trichromatique du nerf optique; Comptes Rendues, tome 121, pp. 1165-1167, (1895).
in its support and development. In England Captain W. de W. Abney has directed his researches in visual physiology to the support of the three component hypothesis, while in America, during the nineteenth century, the most prominent figure was Professor Ogden N. Rood of Columbia University. We shall consider the so-called Young-Helmholtz theory, as reconstructed and amplified by these thinkers, at a later point in our discussion.

The visual hypothesis first definitely stated by Ewald Hering, professor of physiology in the University of Leipzig, takes its origin in the writings of J. W. Goethe, the great German poet, upon the subject of optics. Goethe's work, "Zur Farbenlehre," which appeared in 1810, was intended as a refutation of the then newly proposed theories as to the nature of light. Although the purpose of the argument presented by Goethe was physical analysis, the actual basis of it was a psychological analysis, and hence the end which the author had in view was not realized, -- but in its place there followed interesting and important developments in physiological theory. Goethe's assertion that the qualities of light could be reduced to no less than six fundamental attributes, like Young's original suggestion, received very little attention until the middle of the century. In 1865, however, Ernst Mach, the eminent German physicist, read a paper before the German academy in which he pointed out the inevitable physiological significance of the differences which exist between the visual qualities: red, yellow, green, blue, white and black, and made this the ba-

1 MACH, E.: (Title not found); Sitzb. d. k. Akad. d. Wiss., (1865), Bd. 52, Abth. 2, S. 320.
sis of an opportune study of the psycho-physics of visual sensation. It was not, however, until 1874 that Hering published his *Zur Lehre vom Lichtsinne*, in which the psychological and psycho-physical results thus emphasized were made the foundation of a new and complete hypothesis concerning the neural mechanism underlying visual sensation. Hering's hypothesis has been developed in the course of his own researches since that time, and has also received support at the hands of such of his followers and pupils as Carl Hess, Franz Hillebrand and A. Tschermak. As taught by Hering himself in his newer work, *Grundzüge der Lehre vom Lichtsinn* (1905 and 1907, still incomplete), the hypothesis scarcely differs in any regard from its original form. Others, such as Professor Hermann Ebbinghaus (Breslau) and G. E. Müller (Göttingen) have attempted to make additions or modifications. Concerning the details of Professor Hering's hypothesis, we shall later have more to say.

The Experimental Study of Visual Response.... We have sketched the history of the two leading theories of visual sensation previous to a consideration of the experimental aspect of the progress of this branch of physiology for the reason that both of these theories can be traced to suggestions made at the beginning of the century the events of which we are now discussing. Is it necessary, however, to outline briefly the line of development taken by empirical research during that century, as well as, finally, to mention several other significant contributions to the theoretical interpretation of the phenomena which have been experimentally described. The study of the subjective processes of vision begins with the work of Johannes Evang. Purkinje whose two volumes entitled *Beobachtungen und Versuche zur*
Physiologie der Sinnesorgane, published in 1823 contained a vast amount of data upon the subject of the visual consciousness and its contents. This work laid the foundations of our knowledge of entoptic phenomena, mechanical stimulation of the retina and of the facts of adaptation, including the first notice of the important phenomenon which now bears Purkinje's name.

Of still greater importance, however, was the contribution made by Johannes Müller to the study of the visual process. His work Zur vergleichenden Physiologie des Gesichtssinnes des Menschen und der Thiere, 1826, is regarded by Helmholtz as the pioneer publication in the exact analysis and description of visual phenomena. It marks the beginning of the doctrine of specific nerve energy, and of the comparative anatomy as well as physiology of the sense organs, and soon bore fruit in the way of further writings of a similar character, as, for example, the Beiträge zur Anatomie und Physiologie der Sinneswerkzeuge des Menschen und der Thiere of Gottfried Reinhold von Treviranus, a man eminent in the general development of biological ideas. In 1830 appeared Müller's Ueber die phantastischen Gesichterscheinungen, another important contribution. Other significant "Beiträge" of the ensuing decade were those of Caspar T. Tourtual (1830) concerning entoptic appearances, and F. Arnold (1832), C. M. N. Bartels, (1834), Alfred W. Volkmann (1836) and Ludwig A. Kraus (1837) on general problems of visual physiology. In this decade, also, appeared some of the studies of the unfortunate Fechner, who, in 1839, was forced to resign from his professorship of physics at Leipzig, on account of an affection of the eyes which had resulted from a too constant application to the experimental study of his own visual processes. His epoch-making Elemente der Psycho-
physik, however, was not printed until 1860, the earlier period of his scientific and philosophical career being largely devoted to the study of binocular phenomena and after-images. Chevreul's (E) Lois du contraste simultane des couleurs, which was issued in 1839, was an important volume.

Two of Johannes Müller's most distinguished pupils, E. du Bois Reymond (1818-1896) and H. von Helmholtz, derived from the teachings of their master a marked interest in the problems of visual physiology. Du Bois Reymond's remarkable investigations into the electrical phenomena of muscle and nerve began in 1840 and resulted finally in the publication in 1848 and succeeding years up to 1884 of his many Researches on Animal Electricity, in connection with which he recorded some observations upon the effect of electrical stimulus upon the eye. The great treatise by Helmholtz, Handbuch der physiologischen Optik appeared in three parts, the first in 1856, the second in 1860 and the third in 1866. The experimental and theoretical work which led to this publication began while he was professor of physiology at Königsberg (1849-1855), was continued at Bonn (1855-1858) and at Heidelberg (1858-1871), in each of which universities he occupied the chair in physiology. Besides a comprehensive summary and analysis of all of the work done upon the subject of visual physiology up to his time, we owe to Helmholtz the greater part of our exact knowledge of the dioptrics of the eye, of binocular vision, and the foundation of the quantitative study of color. Helmholtz also designed many of the optical instruments now largely employed in the investigation of visual phenomena, including the Helmholtz color-mixer, the ophthalmoscope, and the ophthalmometer.
Consequent upon the writings of Helmholtz there was a marked acceleration of interest in the problems of the physiology of vision. The number of publications and researches during subsequent years increases very rapidly. For every article or report upon the subject in the years previous to 1860 there are to be found thirty in the last years of the century. Needless to say, it will be impossible within the limits of this thesis to point out the line of historical development which is undoubtably discoverable in the mutual relations of these multitudinous researches and speculations. It will be sufficient to briefly indicate some of the most significant ideas which have evolved since the time of Helmholtz, and to mention the names of the most prominent workers only. Practically all of the experimental and theoretical advances in the field of visual physiology and psychology have been made by Germans or in the laboratories and libraries of German universities.

Experimentation with Pure Spectral Lights

One of the most important lines of investigation which has characterized the Post-Helmholtzian period is the quantitative study of visual response when the retina is stimulated with pure or homogeneous lights of known quality and relative intensity. This type of experimentation has been developed to a very great extent by Arthur König, Johannes von Kries, and their collaborators, using the Helmholtz apparatus, above mentioned. The quantitative study of "color-mixture was begun in 1853 by H. Grassmann, who in that year formulated his three well-known laws of color-mixture. The problems involved were immediately taken up by Helmholtz and his pupils, as well as by J. Clerk Maxwell, the
distribution of complementary lights in the spectrum and the curves of the so-called fundamental sensations or excitabilities postulated by the Young-Helmholtz hypothesis being determined. Under the direction of Helmholtz, G. E. Müllerm determined the laws which govern the relative luminosity of mixed and pure colors, and subsequent and similar researches by König, Eugen Brodhun, Conrad Disterici, and others have yielded exact measurements of many visual quantities, such as the changes of the relative brightnesses of the spectral colors with change in the light intensity (underlying the Purkinje Phenomenon), the sensibility of the eye to changes in hue in various parts of the spectrum, etc. Upon the basis of measurements of this sort the Hering and Young-Helmholtz hypotheses have been given a form more or less quantitative in character. In England, experiments involving the mixture of pure spectral lights have been carried out by Abney, Lord Rayleigh and a few other investigators.

The Study of Color-Blindness...

In connection with their determinations of the visual constants for normal eyes, König and his school have made a detailed study of the properties of the so-called color-blind eye. As a result they have been able to define four or five distinct types of visual response and to point out the relations existing between these and normal vision. The knowledge of color-blindness began, as is well known, with John Dalton's description of his own case in 1794, when he read a paper entitled extraordinary facts relating to the vision of colours, before the Manchester (Eng.) Literary and Philosophical Society. Helmholtz employed Young's hypothesis in the explanation of the facts of color-blindness, but the modern quantitative work tends to show that the conditions
underlying these facts are more complex than Helmholtz was led to believe. The most important modern contributions to this problem of the anomalies of color vision are undoubtedly the research by König and Dieterici reported to the German academy in 1886, and described in full in the Zeitschrift für Psychologie und Physiologie der Sinnesorgane in 1893, and whose investigations have been carried out by Abney, while a great many descriptions of color-blindness in more qualitative terms have been communicated by a large number of observers, among whom Hering and his school are important.

The Functions of the Rods and Cones

The most indefatigable investigator and writer among modern physiologists upon the subject of vision is undoubtedly Professor Johannes von Kries of Freiburg im Breisgau. Von Kries' contributions began in 1877 and have not yet come to an end, and although they touch upon nearly every aspect of visual sensibility, they have largely been concentrated towards the proof of the independent functional value of the retinal rods and cones. The notion that these histologically different elements of the retina might possess diverse functions was first suggested by M. J. S. Schulze, in 1866. He observed that the rods were apparently necessary in animals active at night, whereas the cones were essential to daylight activity. In 1876 Franz Boll, writing under a title

3 Die Anomalen trichromatischen Farbensysteme; ibid. Bd. 19, S. 63. (1899).
identical with that of Schulze's original memoir, reported his
discovery of a light sensitive substance, the visual purple,
in the retinal rods. 1 The chemical and photo-chemical proper-
ties of this substance were immediately and thoroughly investi-
gated by Professor W. Kühne of Heidelberg. 2 Kühne and others have
determined the absorption spectra of the visual purple and its
decomposition products, as well as its rate of bleaching under
different spectral lights. Now the work of von Kries has been
largely directed to the proof of the proposition that the visu-
al purple, as the specific light sensitive substance of the rods,
is the mediator of the gray sensation quality characteristic of
vision at low intensities of illumination. This work has invol-
ved a very careful study of the differences in visual function
which can be demonstrated to exist between the center and the
periphery of the retina, for in the former the rods are absent.
It appears that the Purkinje phenomenon and other striking pe-
culiarities of the visual process are to be referred to the rods.
The contributions of von Kries to this subject have been of such
a character that it may fairly be said that his point is now
demonstrated for good and all, and it is therefore one which we
shall discuss in this thesis only in so far as enters into other
special considerations as a datum. Von Kries' views are fully
set forth in his article in the Zeitschrift, Ueber die Funktion
der Netzhautstäbchen, 1896. 3 Others who have experimented and
speculated concerning the special functions of the rods and
cones are V. O Siven (1905), O. Lummer (1897), H. Parinaud (1887),
Augustin Charpentier and Mrs. Christine Ladd-Franklin. The

1 BOLL, FRANZ: Zur Anatomie und Physiologie der Retina; Arch f.
Anat. u. Physiol., (1876).
2 KUHNE, W.: (Title not found); Untersuchungen aus dem Physio-
(over)
logischen Institut d. Univ. Heidelberg, (1877), Bd. 1, Hefte 1, 2 u. 3.

3 KRIES, J. v.: Ueber die Funktion der Netzhautstabchen; Zeits.
f. Psych. u. Physiol. d. Sinnes., (1896), Bd. 9, S. 81-
124.
first successful attempt to correlate the characteristics of the visual purple with specific visual phenomena was undoubt-
ably that of Parinaud, in 1881 and 1885.

Other Experimenter and Theorists...... We may close this brief review of the history of the study of the phenomena of vision, by a mere mention of certain personalities and their theories or discoveries. One of the most diligent students of color blindness in the middle of the century was F. C. Donders, whom we notice here as the propounder of an hypothesis concern-
ing the visual mechanism which we shall later discuss more in detail. Donder's work was largely done in the seventies and eighties. In the experimental investigation of retinal fatigue and after-images, during the last decade of the century; the names of G. J. Burch and Shelford Bidwell are prominent. Other well-known English investigators are John B. Haycraft--on the Purkinje and other phenomena--, and Sir James Dewar and John G. M'Kendrick--on the electrical changes occurring in the stimulated and unstimulated eye. F. W. Edridge-Green has also written a great deal concerning color-blindness and has brought forward a new hypothesis to explain color-perception.

Alarik Frithiof Holmgren, a Swedish physiologist, must be men-
tioned as a pioneer in the practical study of color-blindness, his work commencing in 1875. Other eminent German investi-
gators during the last century, were H. Aubert, whose Physicolo-
gie der Netzhaut was a notable contribution to existing volumes on the subject of visual sensation and appeared in 1864, -- Sigmund Exner who was one of the earliest students of retinal inertia, -- Adolf E. Fick, and Dr. Guillery, who has made an ex-

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1 PARINAUD, E.: (Title not found); Compt. rend. Acad. d. sc., (1861), Paris, tome 93, P. 286; and ibid. tome 101, p. 821.
haustive study of visual acuity and campimetrical problems. Important contributions to the theoretical—or, more strictly speaking the hypothetical—aspect of the science have been made by the investigators mentioned above and by Mrs. Christine Ladd-Franklin, W. Nicati, Professor Wilhelm Wundt of Leipzig, Professor Hermann Ebbinghaus of Breslau, and W. Preyer.
1. HAPPE, L.: Ueber den physiologischen Entwicklungsgange der Lehre von den Farben; (1877); Leipzig; 44 S.

2. KNAPP, H.: Die geschichtliche Entwicklung der Lehre vom Sehen; (1879); Wiesbaden.

3. MAYER, A. M.: The History of Young's Discovery of his Theory of Colors; (1875); Am. Journ. of Sci. and Arts, April. 1875.


5. PRIESTLEY, JOSEPH: History and Present State of Discoveries Relating to Vision, Light and Colours; (1772); Lond. German trans. (1775); by Klugel, Leipzig, 89 S.


The Evolution of Scientific Concepts. Every science develops from naive beginnings. Primitive scientific concepts are thus simply those of common sense and common thought. As a science advances, certain of these concepts tend to be eliminated and are, perhaps, replaced by new ones, while others are 'amplified or are made more definite. The degree in which the concepts of any science are definite and are separable from those of the naive consciousness is a measure of the age and of the state of perfection of that science. Now many branches of science have already, at the present day, attained an advanced stage of evolution in this regard. Such sciences, for example, are those of dynamics and of electricity.' With them, however, the science of visual sensitivity, certain of the contents of which we are to consider in this thesis, is at present only to be contrasted.

Departments of Nature. The total subject-matter of science as a whole we shall speak of as nature. Nature in the integral of all the meanings that are available to scientific discussion. Now nature is pluralistic and its parts can be segregated according to their resemblances and differences in such a manner that we find it possible to point out particular departments of nature. A department of nature is simply a group of scientific meanings possessing definite relations of resemblance, contiguity, or logical dependency with respect to one another. Nature as a whole may be discriminated from things which are not nature by the criterion of observability. The
contents of nature are all either actually or conceivably observable, and science, the description of nature, thus depends wholly upon the experimental method for its final justification. Nature is not a concrete reality, but is, rather, a construction of the human function of perception, which gathers together the fragmentary impressions which constitute experience and integrates them into a unitary and continuous system. Nature is not, then, necessarily made of "facts" alone; it is made of "facts" and all of the ideas (images) which we require in the synthesis of the "facts" into a system. Nature is a system; its departments are systematic factors in the greater cosmos of which they are parts. Nature never exists, in the proper sense of that word; existence is measured in terms of momentary individual forms of consciousness, and by the sum of those particularized and self-sufficient entities which are objective with respect to these conscious individuals. Concerning objective reality science has nothing to say; that is the province of metaphysics.

The Denotation of the Word Theory

In the course of this thesis we shall have occasion to employ two words having a very general epistemological significance. These are the words: theory and hypothesis. At a later point in our discussion we shall consider the meaning of the word hypothesis in great detail. In this paragraph let us define several applications of the word theory. When we employ the phrase: the theory of D, where D is any department of nature, we shall denote a maximally convenient and concise description of D. The theory of any department of nature is simply the best account we are able to give of it and, of course, its contents. The theory of D differs from the science of D only in being formal; a the-
ory has no element of research in it; a theory is static, congealed. Otherwise, scientific theory and science itself are the same. Now we shall distinguish carefully between the theory of D, and a theory of D; these two phrases are to possess distinct meanings. It is clear that there can exist but one description of D which can be called the theory of D, not on account of the singularity implied in the phrase itself but on account of the definition of the phrase; it is unlikely that two equally convenient and concise descriptions of D could be evolved. However, we can imagine the existence of a large number of descriptions which are more or less convenient and concise, and more or less descriptive of D. These will obviously be related by consanguinity or affinity with the theory of D. We shall therefore speak of such descriptions as theories of D, and any single one of these theories—which may or may no be the theory of D, we shall call a theory of D, the accent being upon the indefinite article. A theory of D is not necessarily a true theory, that is, it is not of necessity a valid description—a descriptive description—of that department of nature towards which it points. Neither is it necessarily very convenient or concise.

The Classification of Theories may obviously be classified in two different ways. In the first place we may classify them according to their actual descriptive-ness, or as we shall say, according to their accuracy. Other things being equal the most accurate theory of D is the theory of D. Secondly, we may classify theories according to their convenience and conciseness. Other things being equal the theory of D will clearly be the most convenient and concise. The em-
phasis is upon the conveniency, of course; conciseness is men-
tioned specifically only because, in the absence of incomplete-
ness, the most concise description is the most convenient, other
things, again, remaining constant. Among theories of any depart-
ment of nature, then, we may discriminate the following types:
(1) the theory of D, (2) an accurate but inconvenient theory of
D, (3) a convenient but inaccurate theory of D, and (4) an in-
accurate and inconvenient theory of D.

The Type of Theories.

of Visual Sensitivity.

Now that department of nature
which we shall later define as the
department of visual sensitivity is one towards the description
of which a great many theories have been offered. A great
many of these theories fall under the fourth type defined above,
and it is now purposed to inquire briefly into the underlying
causes of this fact.

The Necessity of De-
finite Concepts.....

The inaccuracy of current theo-
ries of visual sensitivity rests upon
the vacillatory character of the concepts which are employed.
In our opening paragraph we have already pointed out the likeli-
hood of the existence of such concepts in a relatively undevelop-
ed science. The first essentials of a successful scientific
theory are definite conceptions, that is, words connected with
single and invariable meanings; the meanings are the elements
in nature which are to be the subject-matter of the theory, -- in
the theory they will constitute the department of nature des-
cribed--; the words make up the substance of the theory. In the
particular department of the description of nature which is en-
tered in this thesis, there exist a very small number of defini-
ite conceptions. As in many other branches of biological sci-
ence, there are synonyms galore, and no two writers upon visual sensation employ the same terminology. This is exceedingly unfortunate, for the reason that an accurate and concise theory of visual sensation cannot possibly be constructed if the meanings of particular words, and the words for particular meanings are not constant. Now only will readers of the theory be uncertain with reference to what is signified, but the writer and scientist himself is apt to become lost in his descriptive efforts, for lack of knowing what he intends to express. It is a lamentable fact that scientific literature is not, now, as during earlier periods, written in a single language, -- so that English students of a particular subject, for example, would not be obliged to pour over hundreds of pages of nearly unintelligible German or French, or, otherwise, miss many important observations and ideas by their inability to translate Russian, Italian or Scandinavian. At the present time the universal language, even in science, seems to be impracticable, but it is at least inexcusable that in a single tongue there should exist a dozen names for a single fact without the concomitant existence of a preference in usage. This comes near being the state of affairs in many of the biological sciences. But to remedy this annoying state of affairs is, again, beyond the power of any single thinker. There is, however, one thing which does lie within the capacity of the individual scientific writer, and that is to refuse to employ synonyms in his own writing, and, moreover, to clearly explain the meaning of all the technical terms which he intends using in his essays, and to point out as well as he is able their probable relation with many other expression which have appeared from time to time in similar contexts.
Inaccuracy in Theory Due to Conceptual and to Observational Fault. Now the type of inaccuracy which we have said characterizes many theories of visual sensitivity is that to be referred to an instability of the fundamental concepts of the science rather than to faulty observation. In the development of any scientific theory one first defines his terms, and secondly, he makes observations or experiments in which he determines how these terms should be related with each other in order that they shall properly describe the manner in which their meanings are related with each other. A faulty result may be referred either to an instability of the conceptions themselves or to the inability of the observer to apply conceptions which were adequately stable to the facts of his experience. The most subtle and dangerous fault in any logical structure, scientific, metaphysical, or ethical, is insecurity of ultimate meaning. The writer believes that there is much of this in extant visual theory, and makes its indication his first point of criticism of that theory.

Symbolism in Scientific Theory... It has been said that a scientific theory is a maximally concise description of the phenomena which it formulates. This may be taken to mean, not only that it is a description in the fewest possible words, but that it is a description, also, in the smallest words. There is one method by the employment of which we can, even at the present time, effect an international scientific language, and that is by the selection of arbitrary symbols for scientific meanings, the use of the algebraic method. Bertrand Russell and others, have latterly been very much elated over their discovery

that mathematics is merely "symbolic logic." They might go further and discover that all accurate thinking, apart from the original formulation of observations (physical or psychological) is merely symbolic logic, and that common argument is, when it is thinking, merely a type of mathematics in which the "symbols" which are employed are extraordinarily bulky as well as vague in their denotations. Mathematical is distinguished from dialectical logic merely by the smallness of its words; the distinction between what is qualitative and what is quantitative is perhaps important from a methodological standpoint, but it does not determine the apodictic certitude of mathematical thought. The certitude of mathematical results is an outcome of the accuracy of mathematical logic (the substitution of synonyms) and this accuracy is largely made possible by the simplicity of mathematical words, which we call—as if to demarcate a species—"symbols." This is a convenient term, however, and one which we shall employ, but it should be clearly understood that when for example, we designate a certain meaning by the use of the single letter D, we are simply condensing the verbal elements of our science, and not at all changing its method. The lengthy concatenation of letters: department of nature is equally symbolic in the general sense of that word; it stands for the same ultimate meaning as D. In this thesis we shall make large use of the symbolic method, the details of which will be discussed at another place, but it should be noted here that the employment of this method of denotation neither implies that the meanings denoted are capable of numerical description nor, on the other hand, does it deny the existence of that possibility. Quantitativity and symbolism have no logical connection.
Chapter 3: Some Preliminary Remarks Upon the Hypothetical Factors in Theories of Visual Sensitivity.

The Relation Between Hypothesis, Fact, and Theory.................

A sharp distinction is to be made between the meaning of theory and the meaning of "theory." A theory is a description which pretends to correspond with some specified department of nature; a "theory" is usually an hypothesis. Now we have already indicated that departments of nature contain two sorts of elements: facts and not-facts. The latter we shall speak of as hypotheses. The only difference which need be thought of as existing between an hypothesis and a fact is a difference in the clearness with which the one or the other may be perceived. Facts are obvious elements in nature; hypotheses are natural elements which are not obvious. It is clear that using the word hypothesis in this way we do not designate any doctrine or description, but, instead, some idea or image, which we find to be required in the construction of the scheme of nature. After we have adopted our hypotheses, we still must needs describe them; they are not themselves descriptions, or even fictions. When an hypothesis is described it becomes part of a theory. Hypotheses are a verbal meanings which we are not positively convinced can finally be regarded as integral parts of nature; they are generally of a pictorial nature, and may be considered exemplified in the molecule, the atom and the electron. Psychological hypotheses are possible, however; such an hypothesis is that of the unconscious or sub-conscious mind. We may exhibit the relation which obtains between facts, theories, and hypotheses, in a symbolic
way, as follows. If $H'$ is a description of the hypothetical elements in nature and $F'$ is a description of the factual elements, the theory of nature $T' = H' + F'$. If $N$ symbolizes nature, and $H$ and $F$ symbolize its contained facts and hypotheses, of course we have: $N = H + F$.

Naive Theories of Vision..... Theories of vision, like all other theories, begin upon the basis of naive realism, the belief that visual experience is objective, and constitutes a permanent external world. A blossom, for example, exists, the realist believes, with all its color and delicacy and form whether of not he perceives it; the blossom is not created in his perception, but is, rather, included in it; he does not recognize the psychological nature of space and of sensations of light and shade and tint. The same realistic viewpoint necessitates, of course, the objective existence of the realist's organism. So far the realist is consistent; no one can deny without further investigation, that blossoms and human organisms—although psychological in material—may have objective existence; no possible objection can be raised against the conception of an objective psychosis. But the realist notes a peculiar fact; somehow or other he—realist—that he is—gets an impression of the blossom; he does not note that there is no defensible distinction between an impression of a blossom and a blossom in itself. Thus neglecting a fundamental truth he proceeds to develop a theory of vision. Having made of his perception of a blossom two separate entities, first an impression, and second, an object, and having said that the impression is due to the object, he is forced to explain how an object in space can thrust a replica of itself into consciousness.
Since, also, he has discovered that closing the eyes destroys, or disallows, his impression of the object, he infers that the impression gets into his consciousness from the object via the eyes. Thus there is brought forth the theory that physical objects cast off images, or figured emanations which impinge upon the eye and so mediate the consciousness. An impression is a diaphanous replica of the object which floats into consciousness by the way of the pupil.

**The Career of Naive Theories of Vision.** Naive theories have an evolution by which they become scientific. Essentially this is nothing more than a matter of refinement, of the development of details, making the conceptions mathematical and, as the saying goes, exact. Democritus knew that the image of an external thing must enter his consciousness by the way of his eyes, because closing the lids caused the thing to disappear. But even Diogenes Apolloniates went farther than this upon the physiological side, for he states that the image must travel along the optic nerve, before it can obtain ingress to perception. By setting up obstacles between the object and the eye it is very easy to determine the path taken by the image external to the body, with greater accuracy; if Democritus had been a bit more of an experimentalist, he would surely have set down the law that images travel in straight lines, and that they radiate thus in all directions from an object. The intracorporeal moiety of the path would have been less easy to ascertain, but the method of determining it would have been—-and is—-the same, the introduction of obstacles to the transit of the image; certain physical and physiological discontinuities make it impossible for the wraith of the object to arrive at its destination
in consciousness; these must, then, be discontinuities in the conducting medium. Arguing in this way we are able, nowadays, to trace the path of the image to the occipital cortex, from which, apparently, it takes a very sudden leap, -- into consciousness.

Having settled the problem of the line of movement of the image, we have before us that of its constitution; what is the image made of? Democritus thought that images were constituted of a congeries of exceedingly subtle atoms, and up to the beginning of the nineteenth century, we have indicated, the Democritian hypothesis, or, as it was then known, the Newtonian corpuscular hypothesis, was quite generally accepted.

Latterly we have taken up with the view originally propounded by Aristotle, that images are formed in the activity, or motion, of a special medium permeating all space, the pellucid or aether. But we have gone somewhat farther than this. Diogenes believed that images were made of air, and he said that these aerial patterns of substantial objects passed unchanged through the eye, and along the optic nerve--which he conceived to be a sort of tube--to the brain. We suppose that images are made of energy, not of air, and we agree with Diogenes that their substance does not change, but not that its exact form remains unaltered throughout its entire journey. Before the ghost of the object encounters the retina, it is a beam of electro-magnetic oscillations; afterwards it is a system of nerve impulses, waves of negativity. Modern theories of vision are concerned primarily with the metamorphoses of the image after it has impinged upon the cornea of the eye.

Hypotheses and This Thesis... The purpose of the above sketch is to show in what way the hypothetical elements
contained in the meaning of any scientific theory come to be
developed, and to illustrate the general nature of these ele-
ments. The modern theory of light is as truly founded upon an
hypothesis as was the Democritian theory. The hypothesis, need-
less to say, does not justify the theory, however; the consonance
of the theory with the facts is its justification; but this is
also the justification of the hypothesis. Now the specific ob-
ject of this thesis is the critical examination of certain ele-
ments of meaning contained in current theories of visual sensi-
tivity, which are wholly hypothetical in character. For this
reason we shall later consider the question of the exact signi-
ficance of the hypothesis for science in general with great care.
For the present it is sufficient to have indicated the superfi-
cially observable relationship which exists, on the one hand,
between hypothetical ideas and theory, and on the other hand be-
tween these same hypothetical ideas and the facts that are also
to be found within the meaning of all theories which have any
legitimate claim upon the scientific attention.
Section II: The Plan of the Present Thesis.

The Unsatisfactory Status of the Theory of Visual Sensitivity

It has been said by a certain student of visual physiology that this, and allied departments of the science are at once the most complete and the least completed branches of biological knowledge, and that, withal, the status of affairs thus represented is very unsatisfactory. The meaning of this paradoxical statement is obvious. There is a great collection of facts pertaining to the department of nature under discussion but very little system; in other words, the theory of visual response is under-developed.

The Unsettled Realm of Visual Hypothesis

Now the systematization of the facts of visual sensation and of visual physiology can only occur through the instrumentation of hypothetical ideas, and at the present time none of the hypotheses which have been brought forward for this purpose have sufficient systematic and explanatory power to command the respect of a majority among physiological and psychological thinkers. Compare the following quotations, one from a psychologist, the other from a physicist:

"The Young-Helmholtz theory was devised to explain the phenomena of color-mixture and color analysis. It does explain them admirably; it explains nothing else. It breaks down in the face of the facts of color-blindness, of indirect vision, of after-images and contrast, of the Purkinje phenomenon, etc. ... Hering's theory is, in actual fact, every whit as adequate to the phenomena of color-mixture as is that of Helmholtz. It also offers a self-consistent explanation of the other phenomena referred to above. It has, further, on more than one occasion, been led to predict a certain state of sensitivity or sensi-

1 GREENWOOD, M. Jr.: Further Advances in Physiol.
ble discrimination, and its predictions have been fulfilled. I do not know what more can be demanded of a psychological theory."

"...in the present condition of disagreement among psychologists the oldest hypothesis of color-vision (the Young-Helmholtz) is apt to continue in favor among physicists.... The Hering hypothesis is well known and is probably universally rejected among physicists. Wundt's hypothesis has a good following among psychologists, but is still very little known among physicists. Without pretending to be a psychologist, I am much more favorably impressed with this hypothesis than with that of Hering."

These two bits of controversy are now fourteen years old, but it does not appear that the situation in visual physiology and psychology is greatly changed. There is still very little agreement upon this critical point of the acceptability of extant hypotheses, and very little certainty as to the relative merits of these hypotheses.

Purpose and Limitations of Our Thesis......... The present thesis is merely a sketch—a series of fragments, as its title is intended to indicate—but its purpose is to break, if possible, new paths in the realm of thought which it enters, and to give some earnest—however faint—of potentialities of theoretical advance which—when realized—will yield the result of a more adequate—and, perhaps, a final—systematization of the manifold phenomena of visual response. It is the belief of the present writer that one of the most primitive and most potent difficulties which lies in the way of advance in this—as in other—fields of biology is the preoccupation of the investigator's mind with purely biological conceptions. Not only does

1 STEVENs, W. L.: The Theory of Color; (1898); Science, N.S., vol. 7, pp. 513-520. esp. 515 and 520.
the physiologist know no physics, but the psychologist knows no physiology, and, as a consequence, the solution of a problem which (like nearly every scientific problem) requires the application of the fundamental ideas of all of the sciences, receives no impetus. The writer does not pretend to possess any remarkable degree of erudition in general science, but his purpose in this thesis has been to make some suggestions pointing towards a profounder and more definite analysis of the probable mechanism of visual response than has yet been consummated.

The Physical Realistic View-point............ The first effort of our argument involves a criticism of the prevailing attitude held with regard to visual and other hypotheses, and a plea for a more realistic point of view. It is believed that the pragmatic epistemology so prominent in the defenses of current visual hypotheses is but a tacit admission of the actually non-pragmatic character of the hypotheses themselves. The physical realistic view-point involves definite pictures of every postulated process, and it necessitates mathematical assumptions. From the standpoint of the personal peace of the investigator these requirements are to be regarded with apprehension, for they are very apt to lead him into tight places and to the facing of definite and final defeat as a successful speculator. But if this is rather hard upon the theorist it is also very good for the progress of science, for it is a stimulant as well as a test. The present writer cannot hope to have avoided with any great cleverness the pitfalls opened by the physico-mathematical method. His knowledge of the fundamental concepts of chemistry and physics is relatively superficial, a state of affairs which must inevitably have permitted him to perpetrate
more than one absurdity. Howbeit, he does not find this fact a reason for personal discouragement or disparagement of the work as it stands.

An Analysis of the Implications of the Chemical Visual Hypothesis. The systematic part of this thesis may be described as an attempt to develop the details of the chemical hypothesis of visual response. This has for a long time been the type of the standard visual theories, but, probably for the reason above suggested, no adequate presentation of the implications and consequences of chemical postulates has appeared. Lack of time has made it impossible for the writer to give more than a dogmatic statement of the conceptions in terms of which he has been thinking, and of the explanations which have occurred to him. The few points (e.g. Fechner's law and the question of the inertia of visual response) which have been considered somewhat in detail must be regarded as illustrations of the method of attack which may--it is believed--be successfully applied in the explanation of a hundred other phenomena of visual response. The explanations of after-images, contrast, etc., are cursory only, and the attempt to consider color-blindness from a genetic standpoint may be looked upon merely as a series of suggestions. The writer has adopted the hypothesis of a five-fold retinal excitation partly because he has not come upon any defense of such an hypothesis in the literature, and partly because it seems to him to possess definite advantages of simplicity over the "three component theory."

Psychological History of the Thesis........

A word may be said with reference to the history of the develop-
ment in the writer's own mind of the conceptions employed in this thesis. In general, this development has been notably straightforward and naïve. For example, the postulation of an increase of ionization in the retinal elements as the essential stimulation process did not, as might be supposed, take origin in the search for a device to explain the electrical variations occurring in the stimulated eye, or—on the other hand, in the attempt to provide a rationale of simultaneous contrast, but, instead, was the simple result of an effort to understand how light—an electrical activity—could be effective in the retinal substance. It could only become so in the presence of electric charges, —and immediately the postulation of photo-ionic dissociation was made unavoidable. In another place, the postulation of such concepts—or hypotheses—as impulse loss, cortical dissipation, etc., was quite free from the influence of the idea of specific explanatory consequences. The five molecular resonators are the direct outcome of the attributive analysis of the elementary visual sensation (page 85). The mechanism of complementation, on the other hand, is a pure expedient.

An Apology. Finally the writer desires to apologize

for the generally incoherent and unsystematic character of his work. This is primarily due to haste. A similar excuse must be offered to satisfy explain certain too prevalent lapses from proper grammatical form, good rhetoric, and orthography.
Science Describes Analytically the Monotony of Human Experience.

It is the business of science to describe human experience in terms that are maximally meaningful. Now the two most obvious facts with regard to that experience are its complexity and its monotony. Life is made up of many parts, but of parts which are repeated. It is possible, then, to analyze experience, to point out all of the many elements which together constitute it, to discover their repetitious modes of combination, and to make a record of these discoveries in terms of the results of the analysis. Such a record—in part—is science; a record of the sort we call a description.

Descriptive and Exact Sciences. Sciences have sometimes been divided into two contrasted classes, the exact and the descriptive. For example, it has been said that physics is an exact science, while biology is a descriptive science. By this it is meant that the former is mathematical in its method while the latter is not. This may be the case, but the fact does not make the distinction between the two sciences categorical, for it amounts merely to a classification of the one as more accurate, the other as less accurate. In the most acceptable usage of the word, the descriptive character of physics is greater than that of biology on this very account. A mathematical description is none-the-less a description, and it differs from a non-mathematical description only in its capacity to specify with smaller chance of error, what is meant. The sciences are
all descriptive, but some describe precisely while others only describe approximately, their subject-matter. A pure science in an advanced stage of development is a pure description, and it is also, inevitably; a description in mathematical terms, because the evolution of a science is simply an increase in the precision of its descriptions.

The processes underlying and making possible a description of experience may here be noted. Since a scientific description is based upon an analysis of experience and since it is a record of the repetitious combinations occurring in that experience, it must always be in itself, more or less complex, and thus be itself made up of elements. The constituent elements of a description are what the epistemologist knows as conceptions. Every conception, also, is a compound of two or more parts, and whatever the number of these parts, they can always be divided ultimately into the sign and the meaning of the conception. The sign is usually a word, and the meaning may be anything not a word; every conception contains a verbal element and an aural element. Since descriptions are made up of conceptions and of nothing else, the process by which conceptions are formed is of basic importance to science, which is a descriptive endeavor. This process is that called definition.

Definition is the fundamental prerequisite of scientific progress. An aggregation of signs or sounds becomes a description when the signs and sounds have all been defined, or have been provided with meanings. It should not be imagined that definition is a process which can be com-
pletely represented by the use of words, for if it were such a process it could not be made the basis of description, since in itself it would be nothing different from description. Definition is always in the last analysis the process of connecting a word with some element of experience which is not a word, which, in fine, has in itself no meaning. Such an element of experience the epistemologist speaks of as averal, and the process of connecting a verbal with an averal element of experience is spoken of as exemplification. Science is, then, a representation of the repetitious combinations of averal elements occurring in human experience, by the use of verbal elements. A representation of this sort may be spoken of as a symbolic representation.

The Purpose of Science ...... Why, we may enquire, do we undertake the development of such a system as science? The answer is that we do this because we perceive that the possession of formulae representing the constant modes of union between different factors of our experience will enable us to interpret one of those factors as proof of the presence or potential presence of the others, so that when--as is usually the case--the form of combination of the factors is in time rather than simply in space or in consciousness--we can, in general, through action, avoid or seek those other factors, if they are desirable or undesirable. The quest for science thus rests upon a utilitarian basis. We seek the perfection of science because we believe that when attained it will aid us in making life more worth living.
Chapter 5: Symbolism and Thought.

If the final object of the exist-
ence of a science is merely the fur-
therance of human activities in the
quest of forms of experience which are not necessarily scienti-
fic but simply desirable—or relatively desirable—in themselves,
it follows that the only form in which science can be regarded
as perfect is that form in which it is easiest to apply in any
specific situation, and in which such an application yields max-
imally desirable results, that is, leads most surely to the re-
sults anticipated in its employment. We have pointed out in a
preliminary discussion (cf. page 22) that this circumstance
makes it necessary to assert that a science is fully developed
only when its descriptions are mathematically exact, and when
they are most concise. But there is another—and more important
result which flows from the requirement that a science—a sci-
entific theory—be made as convenient as possible. This is the
result that, besides describing experience, science must describe
certain constructions of meaning which are not in experience at
all, as it is originally presented to us. These constructions
are what we have chosen to denominate hypotheses; they enter in-
to scientific meanings and thus become an important part of na-
ture because of the fragmentary and unsystematic character of
experience pure and simple.

Filling in the Blanks in
the Experimental World...

Science as a description of
pure experience would simply be a
record of disconnected sensations, images, and perceptions. Such
a record might conceivably be moulded into a system without the
interpolation of any meanings beyond those immediately apparent in the experience itself. But as a matter of fact when we attempt to construct a system of pure experience we fail. The experimental world is like a page of philosophy from which half of the words have been dropped. If we try to make sense out of the residue without "reading between the lines" we have very little success. If, on the other hand, we endeavor to find certain words and phrases which will fit harmoniously into the lacunae of the page we may discover the significance of the whole. Such a filled in and completed page of philosophy will more easily comprehended, remembered and utilized, than the fragmentary and unintelligible printed matter with which we were originally presented, no matter how clever a scheme we may have devised for remembering the order of the words. Such scientific conceptions as the molecule, electricity, force, aether, etc., are meanings which have been interpolated into an experiential description which is so full of blanks that it is almost entirely unintelligible.

The Pictorial Element in Thinking

In the application of scientific theory to experience, we are forced to deduce results appropriate with respect to special cases from principles which are themselves general. It has been suggested in a preceding discussion that this process of scientific thought may be made wholly formal, depending simply upon the substitution of symbols in equations. In so far as we regard thought as a conceptual process the above characterization of its method is certainly valid, but thought, thus defined, is inseparable from perception, and while some of our symbolic logic is based upon that sort of perception which is given in pure experience,
a large part of it, in a system of nature, must be founded upon imagination; that is, in the determination of the relations which are to be described as existing between the ultimate elements of meaning involved, we must draw a picture, either actually or in the "mind's eye," and "see" what must be postulated. Thus in reasoning concerning thermo-dynamic processes, instead of thinking in terms of temperature sensations, or the position of the mercury in the glass, we employ the molecular conception, because its utilization leads most quickly and easily to the results which we desire, but if we need to know what will occur under certain primitive conditions in a molecular mass, we must find out by use of the imagination, for there are no molecules in pure experience. Thus in all advanced scientific thinking there is a very important pictorial element. The point is that the "pictures" are more useful—more exact, concise and easier to employ—than any purely formal system involving nothing but words and pure experience; hence they are more scientific. The ideals of science, itself, force it to do more than simply to describe experience as it comes and to make an exclusive system of experience; the most pragmatic of scientists cannot progress without the postulate of nature.
Chapter 6: The Scientific Merits of Physical Realism.

Vacillation in Visual Hypothesis......

The foregoing remarks have been made with a view to the discussion now to be entered, and which we shall call a defense of physical realism. The point of view commonly taken by those who advance or defend special hypotheses of visual response is that of the radical pragmatist; a visual hypothesis is true scientifically in so far as it resumes the phenomena of vision, in so far as it helps us to formulate, to correlate, the empirically established facts. A process which presents so many complicated factors cannot be comprehended—grasped as a whole—without some sort of a picture to assist one. This picture of an underlying mechanism is given in the hypothesis; it is a true picture in so far as it permits an harmonious inclusion of all of the data of visual psychology and physiology; it can be true for no other reason. As an illustration of this pragmatic attitude the following passage from a recent exposition of Hering's hypothesis, may be quoted.

"It is further to be noted that the four physiological 'substances' have just as much and just as little real existence as the three components of our other theory [the Young-Helmholtz]. It is idle to say that the postulated anabolic and katabolic processes are essentially unlike any chemical mechanisms with which we are acquainted. It is equally vain to object that stimulation processes in animal nature are, to all appearance, bound up with katabolic changes; this would be a valid objection if we tried to identify the hypothetical substances with any known retino-cerebral constituent. No such identification is attempted; the suggestion that Hering and his school identify the black-white substance with the visual purple is altogether false. The fact is that this theory can only be judged on the grounds of scientific expediency, and in no
other way. Does this method of presenting the facts give us a clearer insight into the phenomena of vision than the method based upon stimulus relations? This is the only question which requires to be answered."

It is because of this pragmatic attitude that we find both the disciples of Hering and of Helmholtz unwilling to localize their hypothetical "substances." At one time the metabolizing bodies of the Hering theory are spoken of as though central, at another as if peripheral in position, and the consensus of opinion is that it makes no particular difference whether we treat them as retinal or cortical, so long as the idea of them aids us in our empirical research and practical activities. Mrs. Ladd-Franklin looks upon her hypothesis in the same light; concluding her introduction in the original paper, she says: "I present the following hypothesis not as a finally valid hypothesis of light sensation but rather as a symbolic representation of an hypothesis the form of which can in some measure satisfy our logical requirements." The Young-Helmholtz hypothesis has been epitomized in the following words: "The effect produced by any chromatic stimulus is supposed to depend upon the resultant changes set up in three independent "substances"; nothing whatever being postulated with respect to these substances except that the magnitude of change in each is a function of three independently variable stimuli in terms of which the given stimulus can be expressed." Such a construction cannot even be legitimately termed an hypothesis; it is nothing more than a symbolic formulation of the facts of the psycho-physics of the

2 LADD-FRANKLIN, C.: Zeits. f. Psych... Bd. 4, S. 214. (over)
3 GREENWOOD: loc. cit., p. 405.
mixture of spectral lights.

Illustrations of the Value of Hypotheses and Their Nature.... Now from a strictly scientific point of view the pragmatic methodology is the only one which can be consistently defended. Science is defined as a systematic description of phenomena, with whatever aids are requisite, and as such it cannot attempt to describe any supposed realities, non-phenomenal in character. Whenever the scientist thinks of molecules, electrons and unseen mechanisms of any sort he does so only as an aid towards the correct formulation of the facts which come concretely into his experience; the bright spot upon the wall of a vacuum tube is a fact of our perceptual consciousness; the cathode rays—the flying electrons—are not, and we think in terms of them only because they enable us to bind together a hundred different observations which—in addition to the bright spot on the tube—have been made in connection with induction coils and glass vessels under varying conditions. We know nothing by experience of "electricity"; all that we can study experimentally are electrical phenomena. Similarly, the various light sensitive molecules which are postulated in chemical hypotheses of visual sensitivity cannot be regarded as of any final significance from a scientific point of view apart from their intimate conceptual connection with the phenomena of visual psychology and physiology. No molecular image can at present be regarded as having been distinctly realized in direct perception. The scientist thinks in terms of molecules because the mechanism of human thought demands "substantial and tangible" images, and because it is found that the use of these images
permits the attainment of conclusions which are verified in concrete experience.

The Absence of Any Ultimate Alternatives in Physical Hypothesis........

If what we have said above is epistemologically tenable, in what way is it possible to adversely criticize the pragmatic viewpoint with reference to hypotheses of visual sensitivity? Well, there are two facts which make it possible to do this and to a consideration of these we must now turn. In the first place it is to be noted that although the pragmatist is constantly insisting that it is possible for a number of different ideas to be simultaneously and equally true if they are both equally consonant with the facts of experience and with the demands of practical life, it never happens, in point of fact, that more than one idea is found to be acceptable—even upon a pragmatic basis—when the phenomena which the competing ideas are supposed to explain are exhaustively studied, and when the utility of the ideas is rigidly tested. In the struggle for existence between ideas there is finally but a single survivor; the victor stands alone; and the victory is seldom, if ever, won "by a neck"; the other contestants are wholly outclassed. Those departments of investigation in which there exist a multitude of equally valuable fundamental and competing conceptions are those in which data and methods of research are most scanty and undeveloped. And as the various branches of science grow in perfection, the underlying hypotheses of each branch may be observed to approximate those of other, and especially adjacent, branches. This happens for the reason that hypotheses of a particular sort appear to be so vastly more use-
ful than those of any other possible sort that the other hypotheses possess in the end not a ghost of a show. It appears, then, that from a purely pragmatic standpoint, the character of the ideas which we employ as aids in the formulation of experience is necessarily limited in a definite and particular way. There is but one finally acceptable hypothesis in any field.

The Basis of Physical Realism and Mathematical Definiteness in Hypothesis

It is noted that as a science advances and its hypotheses become more definite and specific, they also become mathematical in character; the atoms and the electron possess definite mass, shape and volume, and move at definite velocities, occupy definite positions in space, etc. It is obvious that if the above conclusion is a tenable one—that only one hypothesis is ultimately defensible—the hypothetical or imaginative aspect of a science develops in exactly the same way that it would develop if there existed an actual, definite and constant physical mechanism which it is the function of the hypothesis to represent. It is, however, perfectly clear that such a mechanism does not exist in our experience, and from the standpoint of science if it does not exist in experience it does not exist at all. While admitting this to be the case it still appears desirable that we should attempt the development of hypotheses in general as if we believed in the real existence of the mechanisms which they represent. If we do this we shall be led to make our descriptions definite and mathematical and of a type consistent with the final form of the actually acceptable hypothesis. But the principal merit of definiteness in hypothesis lies in the definiteness of the consequences which follow
from its assumptions, and not only the definiteness but the number of these consequences. On account of the specific implications of the specific idea, the idea itself is sooner forced out of the battle by the failure of these implications to conform with the facts, while an hypothesis whose logical consequences are vague and shifty may remain in the field, because its definition is so inadequate that it cannot be brought into comparison with all of the known empirical facts.

The Study of Visual Phenomena Will Be Aided By Metaphysical Conceptions......

For the above formulated reason alone it would seem advisable to take a realistic point of view in the development and criticism of visual hypotheses, but there are further and more cogent reasons for doing this. It has been said that from a purely scientific standpoint hypotheses cannot be regarded as anything beyond an aid to formulation and practical activity. But the processes of visual response cannot be adequately considered from a purely scientific standpoint; a metaphysical reference, while theoretically avoidable, actually exists in every psychological experiment, and for this reason it becomes possible and advisable to place the study of visual sensation upon a metaphysical as well as upon a scientific basis.

The Difference Between Science and Metaphysics

Science has been defined as the study of phenomena, the description of experience by the use of words having meanings in experience. But experience is always the experience of some particular individual; experience and the individual are, in fact, one and the same. Every purely scientific observation is a process that goes
on entirely within a single human consciousness, and its results apply to that consciousness, for that consciousness, and in no other way. Science is, in other words, a description of the entire subjective, of the events which are given in the experience of the first person. It is nothing else, whatsoever. Metaphysics, on the other hand, is the study and description of objective existences, of realities— in contradistinction with phenomena— ; 'it is concerned with those events which are given only as parts of the experience of the second and third persons, in short of the objective universe. Now in the study of visual sensation the second person is important, although—let it be admitted—not indispensable. Hence the principles of metaphysical reasoning are apt to be of some value in argumentation concerning visual processes.

The Physical Interpretation of Color-blindness. To illustrate the metaphysical reference which may exist in experiments in visual sensation let us consider the typical examination of a color-blind person. In this examination two individuals are concerned, the experimenter, E, and the observer, O, who is color-blind; it is, in other words, a psychological experiment (cf. page 116) of the usual variety. E is a scientist—a physiologist—who desires to describe the facts of color blindness. From his point of view all facts must be such as form a part of his own experience, and the only facts which he is able to study and to record in his examination of the color-blind person are the states and modifications of his own consciousness during the period of the examination. The color-blind person himself is but a part of the visual and auditory perceptual
consciousness of E, as are the things he says and does. We will suppose—describing the examination in terms of E's experience—that E places before the eye of O the eye-piece of a spectroscope, and receives an oral report of the colors seen by O in different regions of the field. From a purely scientific standpoint E can only interpret the divergence of O's description of the spectrum, from that which he, himself, would give, as a peculiar departure in the mode of co-existence of spectral impression with descriptions resulting from such impressions; O is for E, scientifically, merely an anomalous organism, an organism which reacts differently from the typical organism with respect to certain stimuli. This is because E, as a scientist, believes only in his own experience, in phenomena, in things which appear, --and the visual consciousness of O does not appear.

The Effect of the Metaphysical Postulate Upon The Theory of Visual Response

But suppose that E makes a certain assumption, viz., the fundamental assumption of metaphysics, that O's consciousness—the consciousness of the second person—does really exist and is the cause of the reports which E is receiving. This is the assumption of an objective reality, and with it the situation for E is suddenly and radically altered. In the effort to make comprehensible the deviation of the light reactions of the O organism from the normal, E has been led to adopt the hypothesis of a mechanism connecting stimulation with oral description which is different from that ordinarily to be imagined in connection with the reactions of exemplars of the species Homo sapiens. This mechanism is complete and continuous and furnishes a thorough physiological "explanation" of the pecu-
liar phenomena involved. E realizes that the mechanism, in point of fact—or in reality—does not exist, but he finds that the idea of it aids him in correlating his observations, so he retains it. He has no need of the assumption of the objective visual consciousness. But we have supposed that in spite of this fact, he does make the assumption, which consists in the postulation of a form of existence more or less similar to his own visual consciousness, the elements and attributes of which (objective) existence are correlated (causally) with certain of his own perceptions, viz., the oral reports of C. But a more detailed analysis shows that he has also assumed the causal correlation of this objective existence with certain elements of the hypothetical mechanism of the process; he finds himself obliged to refer the objective consciousness to the hypothetical brain process. There is not space here in which to develop the line of thought which is necessarily attached to this result. Suffice it to say that the fact of the continuity of nature forces E to the conclusion that there exists a complete train of objective processes, paralleling completely his hypothetical mechanism and the facts of his perception, and that in this train of processes the real visual consciousness of C bears the same relation to preceding and succeeding processes that the cortical link in the hypothetical chain of physical events is imagined to bear to the physical processes conceived to precede and follow it. The experience of E in the examination and the hypotheses to which he is led are but symbolical representations of an objective structure and change which constitute the real visual process and of which the color-blind consciousness (C) is a
causally included segment. The elements of this complete objective process are presumably not physical in character, but they are of such a nature as to be correlated point for point with physical events, whether perceived or necessarily postulated. The ideal physical universe of molecules, and other unseen structures and mechanisms, which, as we have shown above, must inevitably be imagined in connecting the scattered facts of human experience, is thus seen to be determined by a real objective universe, which is not physical but which is mathematically similar to the physical universe.

Final Defense of the Realistic Point of View. Since there is very little doubt that in attempting to describe the things which exist in the most accurate terms, and by the use of a method which introduces no artificialities of conception, without reason, we shall be forced to consider every visual process as it really occurs, as a process the actual causes of which are objective, non-physical in character (and of which the imagined physical and physiological "causes" are merely symbolic representations in the mind of some experimenter E) it seems advisable to consider the consequences of this point of view for our discussion. After all, the purpose of our thought is always broader than that implied by pure science, and although the present thesis is in science rather than in metaphysics, it will often prove of assistance to the scientist to recognize the real conditions underlying his argumentation. The most immediate consequences of the above discussion are described in the following sentence. The realistic point of view in the discussion of the hypothetical mechan-
ism of the visual process is desirable because that hypotheti-
cal mechanism when fully and satisfactorily described can only be regarded in any ultimate (antisolipsistic) philosophical analy-
sis as a symbolic and absolutely determinate representation of the real visual process the nature of which in any particular instance is wholly independent of pragmatic considerations and in the description of which there is absolutely no degree of freedom.

Definition of Physical Realism

The doctrine that for all practi-
cal purposes, as well as theoretically, physical hypotheses are finally no more optional in their deter-
mination than are physical facts, we shall denominate physical realism. It defines the point of view to be taken in this the-
sis; the criticism of current hypotheses concerning the neural mechanism underlying visual sensation will be attempted from this viewpoint only. It is believed that if an hypothesis cannot be defended as a physical reality, it cannot be successfully de-
fended at all, and that the appearance of pragmatic argument in attempts to defend certain hypotheses amounts to nothing more or less than an implicit admission that the hypotheses in question are pragmatically as well as metaphysically ailing. The physical realist asserts that while it must be admitted in the last analysis that the hypothetical things and processes of physical theory do not exist, never-the-less recognition of this fact in the course of physical thinking hinders rather than helps the progress of science, because whether they exist or not, the exist-
ing situation is exactly the same as it would be if the things and processes in question were ultimately and absolutely real.
An Hypothesis of Visual Sensitivity Must Be In Harmony With All General Physical Hypotheses.

There is one consequence of physical realism which cannot be too strongly emphasized, and that is the necessity that the hypotheses contained within one department of nature should be in harmony with those of another department. The world of physics is far from being a simple abstract from that of naive realism, for there are no molecules, no atoms, no electrons and electricities in the latter; the world of physics is largely an ideal world which we have built up from the most fundamental and simplest elements of our perception, and the function of which is to serve as an explanation or rationale of that irrational and fragmentary realm of our actual experience. Now one of the remarkable things about this great hypothetical universe of physical science is its continuity; so far as we have gone, nature holds together as a whole; we have reason for believing that eventually the hypotheses underlying all of the phenomena of nature will perfectly unite to form one great hypothesis underlying the entirety of our experience. The presumption in favor of this event is so powerful that the idea of the continuity of nature becomes a norm for our argument. An hypothesis of visual sensitivity is an idea of some process which is to be regarded as a part of the physical world of molecules and motion, and which, in that position, is to serve as an explanation of the observed facts which we group together as the phenomena of visual response. It is evident, then, that such an hypothesis must conform with at least two requirements; it must be consonant with the facts, and it must be in harmony with the fundamental conceptions which
define the physical order. In other words, any hypothesis of vision which makes use of mechanisms and actions inconsistent with the general conceptions and laws of physics and chemistry, or of biology, is, for this reason alone, liable to rejection. No visual hypothesis can afford to contradict the principle of the conservation of energy, the molecular theory, or the theory of evolution; neither can it safely fly in the face of many minor physical principles and hypotheses. If we adopt a non-realistic point of view there exists a constant temptation, however, to neglect these general connections of every scientific idea; for example, it has been claimed (especially by Mrs. Ladd-Franklin) that Hering's hypothesis is anomalous in its physiological chemistry, making use of the conceptions of anabolism and katabolism in a manner out of harmony with general physiological principles, and we have already (page 43) seen the sort of reply which is made to this really significant criticism.
Chapter 7: The Terminology of Hypothesis.

We have defined an hypothesis as a part of nature (cf. page 27); as an a verbal rather than a verbal element of conception. An hypothesis may be regarded either as the idea of an unseen mechanism, or as the unseen mechanism itself. The verbal element in the conception (cf. page 38) of any hypothesis, we shall speak of as a postulate, and the process of forming and adopting any hypothetical conception we shall call postulation. An hypothetical conception = A postulate + An hypothesis. When a particular hypothesis is imagined as continuous with certain experiential facts, we shall say that it underlies those facts. Nature, we have seen (page 28) is a compound of facts and hypotheses; the facts are superficially observable, the hypotheses underlie and support them—at least in our scientific thought. Whenever we find that particular facts—whether or not those with reference to which the hypothesis was first proposed—are in harmony with the consequences of any hypothesis, we shall assert that the hypothesis explains these facts. In order that any hypothesis should be acceptable it must be capable of explaining all of the facts which it is said to underlie.
PART TWO: ELEMENTS OF THE LOGIC OF VISUAL SENSITIVITY.


Definition of a Department of Nature: Visual Sensitivity.

We shall describe the department of nature (cf. page 20) concerning which this thesis is written, as that of Visual Sensitivity. The word sensitivity is chosen instead of (say) sensibility because its native connotations are about equally physical and psychological. We shall employ the phrase visual sensitivity to signify all aspects of our subject, by whatever point of view made possible. The designation includes the entire field to be studied, -- be it physical, factual, phenomenal, psychical, or what not.

Visual Structure and Visual Response.... This field presents two general aspects: those of visual structure and of visual response. The distinction between these two aspects lies in the fact that the latter exhibits the attributes of time and change, and is dependent upon the former, which does not exhibit these attributes, and can be considered apart from visual response. Within the concept of visual structure we include not only the retina, the optic nerve, and the cuneate cortex, but also the visual field, which forms a part of the consciousness of the subject of visual sensation, or of the observer in the psychological experiment (cf. page 116). We may symbolize (cf. page 25) any visual structure by use of the letter Z, and as a synonym (cf. page --) we may employ the term visual apparatus. Visual structure = visual apparatus = Z.
Visual Response. Within the concept of visual response we shall include all of the processes which go on in the visual structures, whether or not due to external forces. But when, as is most common, these changes occur as a result of the impression of some force not originating in the visual apparatus itself, we shall speak of a visual response, and the symbol for any complete causally unitary response, including the acting stimulus and the structural ingredients, is to be $V$. As a synonym we may make use of the term visual process, and when considering this process with special emphasis upon its structural foundations, we shall speak of the visual mechanism. The relation $V = f(Z,t)$ is obviously true; any visual response can be redescribed in terms of the structures of which it is the process, and the time.

Divisions of Visual Sensitivity in this thesis are all facts of visual sensitivity, and our fundamental problem is the development of a maximally probable description of the mechanisms physically underlying these facts. The department of nature thus described may be divided into two completely distinct sections, the psychical and the physical, and the contents of which we shall designate as visual consciousness and visual neurosis respectively.

Visual Consciousness and Sensation

Visual consciousness may be regarded in two lights, as structural and as functional. The structural aspect of visual consciousness will be called the visual field, and may be symbolized by $F$. Its nature will be more fully discussed when we come to con-
sider in detail the psychological aspects of our problem. The functional aspect of the visual consciousness with which we are concerned in this thesis is that of visual sensation, which we shall symbolize by the letter S, and which, again, will be fully discussed at a later point. A second functional aspect of the visual consciousness is that of visual perception, but with this we shall not be obliged to deal.

Visual Neurosis. Visual neurosis, also, can be divided into two contrasted departments, visual neurostatics and visual neurokinetics, the study, first, of the physical structures underlying visual sensitivity and, second, of the processes or changes which occur in these structures. As a matter of fact, the structures in question are non-functional only in dead organisms, and the functions in question are always so intimately dependent upon and, in fact, so much at one with their structural substrates that it seems unnecessary to invent a terminology to distinguish the structure from the process. When, however, it appears advisable to do this we shall employ the term visual neurostasis to signify the structural substrate of any particular visual neurosis. We extend the concept of visual neurosis in such a way that it covers the entire field of visual sensitivity so far as it is physical. As a symbol for visual neurosis we shall employ the letter N.

The Elements of a Visual Response. Since visual response is a process it is possible to classify the facts and hypotheses contained within it by considering their position in the different chronological stages of that process. Making
use of this expedient we may further subdivide and arrange the divisions of the department of visual sensitivity as follows.

The Visual Stimulus... The first element in every concrete case of visual response (V) we shall call the stimulus. It may seem unjustifiable to include the stimulus in the response, but it is believed that, on the whole, nothing is to be gained by drawing a line of categorical demarcation between the intra- and extra-organismal elements of the visual process. We are only concerned with the stimulus when it is within the organism and is so intimately connected with it that to all intents and purposes—and in fact—it is merely one constituent of a single unitary process, that process which we have chosen to denominate a visual response. Now visual stimuli may be of various sorts, but by far the most significant visual stimulus is light. We shall designate any visual stimulus by P, and light, in particular, by L. L denotes the special light which forms the first element in the specific visual response V. At a later point we shall discuss the nature of light in detail; there we shall describe its most important attributes: (1) its composition, P, (2) its intensity, e, and (3) its frequency, n. (cf. page 148)

Visual Stimulation... The second element in every concrete visual response is visual stimulation, X.

This phrase will be used to denote every factual or hypothetical mechanism involved in the reaction of the retina to light or other stimulus. It thus denotes the retina itself so far as it falls within this definition. The most important factors in visual stimulation are the special sensitive structures of the retina, which will severally be designated by M, M', etc.,
where $s$, $s'$, etc. are any convenient subscripts describing the limitations of the sensitivity. The processes which these structures subserve will in general be written as time derivatives of some aspect of the structures, e.g., as $\frac{dms}{dt} = \dot{m}_s$.

Visual Conduction... The third element in $V$ is visual conduction, a term which may be employed to denote the structures and processes intermediate between the retinal and cerebral factors of visual response. Visual conduction has as a structural basis the optic nerve with its ramifications. Viewed as a process visual conduction will be termed the visual impulse, which may be symbolized by $I$. Within the concept of the visual impulse we include every factor in the visual response which intervenes between stimulation and cerebrosis, which is next to be considered.

Visual Cerebrosis... The fourth chronological element in visual response is that of visual cerebrosis, $C$. This word stands for every observed or postulated structure or process which is immediately correlated psycho-physically with the facts of the visual consciousness. We suppose these structures and processes to be those of the cortex of the cuneus a gyrus of grey matter situated medially in the occipital lobe of the cerebrum.

The Fifth and Other Elements The fifth and central factor in the visual response is that of the visual consciousness, with the sensory aspect, $S$, of which we are in this thesis primarily concerned. The nature of this fifth factor will shortly be discussed great detail. In addition to these fundamental divisions of the subject-matter of the science and the
theory of visual sensitivity, there are other special and related departments of nature, certain divisions of which may have to be considered. Such are, for example, the general structure and function of the eye as an optical instrument, and the motor results of visual response.

Special Limitations of the Symbolic Terms..............

We shall limit the usage of the symbols, V, P, L, X, I, C, and S in a special way. V does not signify visual response in general; it always denotes some particular visual response. Now within this specific response are to be found the successive elements: P (L), X, I, C, and S, and the significance of these letters will be limited to a designation of the characteristic parts of the specific response. Thus P is always the stimulus within a particular instance of visual response V, I always an impulse forming part of a special response, etc. Similarly, S is always the sensation resulting from a particular stimulus, P, etc. If we mention one of these factors, we imply the rest, and we imply special instances. Further on we shall delimit the meaning of S so that it will signify the attributes of a point within the visual field. This being the case, after having established the definition of the elementary visual sensation, we shall employ V as the symbol of the elementary visual response, and P, (L), X, I, and C as the specific and corresponding elementary stimulus, (light), stimulation, impulse, and cerebrosis, respectively. The meanings and interrelations of all of these concepts will appear in greater detail as our discussion proceeds. In any event, however, whenever S is spoken of it is to be thought of as "the sensation corresponding with particular factors in a
particular visual response;" it is the S of P, (of L), of X, of I, of C. We may express this idea symbolically in the following manner. Always: \( V = P + X + I + C + S \), but if we speak of a certain \( S = S_1 \), \( S_1 \) must be the final member of the visual response: \( V_1 = P_1 + X_1 + I_1 + C_1 + S_1 \). Usually \( P = L \), so that \( P_1 = L_1 \). This is merely a symbolic representation of a particular sequence of causally related events.

When we say that \( V \) does not stand for visual response in general, we do not mean that \( V \) cannot be employed in a generic sense. \( V \) does not mean every visual response; what it does mean is any visual response. The use of all of these symbolic terms is intended to be entirely similar to that of the symbol \( x \) in algebra and the Cartesian geometry. \( x \) is never every \( x \), but it can at any moment be regarded as standing for any \( x \) whatsoever. \( V \) is a variable, not a class; but, as a variable, it covers all of the members of the class of visual response, and may at any time be employed to signify any member of that class; but when it does this it signifies this member—with all of its specific parts and attributes—exclusively.
Section V : The Elements of Symbolic Logic.

Every concept is made up of two important elements, the symbol or word, and the meaning or thing symbolized. From the standpoint of science the meaning in a concept is the only ultimate justification for the use of the concept; the symbol or the word is important only because of its power to mean. Other things being equal, of two concepts embodying the same meaning, but a different symbol, one may as well be employed as the other. The only point in which they differ from one another is with respect to their contained symbols, but since the purpose of all conceptions is to convey meanings and not to present special symbols; two symbols possessing the same meaning are scientifically equivalent. We symbolize this fact in the equation. If \( C \) and \( C' \) are two symbols having identical meanings, we write: \( C = C' \). This notation signifies that in any context in which \( C \) can be descriptively employed, \( C' \) can also be employed with equivalent descriptive power, that is to say, the sign \( \neq \) gives us permission to substitute a symbol or symbols on the right for another symbol or other symbols on the left of the sign; it indicates a relation of synonymousness.

Now if the only application of the equation sign which was possible happened to be that of the interrelating of arbitrarily defined synonyms we should probably make but little use of it. In point of fact, however, we find it highly useful by reason of a certain peculiarity which is observable in nearly every scientific meaning. This is the peculiarity of complexity. When we carefully
examine the fact or hypothesis in nature which we have symbolized by \( C \), we are apt to discover that it can be split up into parts, or that several or many distinct attributes can be discovered within it. This being the case we may symbolize these parts or attributes, whichever they may be, by the use of new verbal elements. Suppose that we discriminate four different parts in the meaning of \( C \), and that we denominate these parts: \( a, b, c \) and \( d \). Then, obviously, \( a, b, c \) and \( d \) together, have the same meaning as \( C \). We indicate the togetherness by the sign + and the identity of meaning by the sign =, as before, so that we write: \( C = a + b + c + d \). The use of the plus sign in non-mathematical—as well as mathematical—equations depends solely upon the power of analysis. If the meaning of \( C \) is perfectly simple, \( C \) cannot be equated to a logical sum.

The Significance of Logical Subtraction

There are certain cases in which the meaning of \( C \) can actually be broken up into separable parts, these parts still retaining their identity. When this can be done we express stages of decomposition of the meaning of \( C \) by equations of the following variety: \( C - a - b = c + d \), making use of the minus or subtraction sign −. It is always descriptive to employ the minus sign in this way when the meanings in question are capable of an actual decomposition, without a loss of identity of their parts. This is not the case with attributes. It is descriptive to write a sensation as the sum of its attributes: quality, intensity, clearness, etc., but it is not descriptive to subtract the intensity (say) and to then equate the difference to the quality plus the clearness, etc., because subtraction of the intensity of a sensation leaves no remainder.
The Significance of Logical Multiplication.............

The fact that attributes cannot be taken away from that of which they are attributes, with a remainder, leads us to introduce a different symbolism to indicate their relationship with each other and with the total meaning. Instead of regarding this meaning as the sum of its attributes, we may regard it as the product of its attributes, so that if \( a, b, c \) and \( d \) are attributes of the meaning of \( C \) (mean the attributes of the meaning of \( C \)), and none of these attributes can be eliminated without the destruction of the meaning of \( C \) itself, we write \( C = a \times b \times c \times d \). This notation declares that if we make the meaning of any one of the members of the right-hand side of the equation equivalent to nothing, the whole equation becomes an equation of nonentities. The general logical significance of zero, \( 0 \), may here be noted; \( 0 \) is the only symbol employed in scientific theory which is without meaning. When we say that \( C = 0 \), we assert that \( C \), also, has lost its meaning, and hence that it will no longer be employed in discussion. A logical product is always the outcome of what we shall call an attributive analysis of a scientific subject-matter. This sort of analysis is to be distinguished from an actual analysis, the results of which are expressed by means of a logical sum.

The General Significance of Functionality...........

In addition to the method of symbolizing differences which are observed to exist between the meanings of scientific words or symbols, a matter which will be discussed in the following section of this thesis, there is another symbolic device which requires mention. That is the so-called functional relation. The
most general result of the scientific analysis of nature is the belief that nature must be regarded as a causally ordered system. This simply means that the parts of nature are not independent of each other in quality or action, but that on the contrary they mutually determine each other. Given $A$, $E$ must also be given. This relation of interdependency which can be demonstrated to hold between different parts of nature is summed up in the concept of functionality. If $A$ and $E$ are two mutually dependent parts of nature, i.e., mean two mutually dependent parts of nature, we write: $A = f(E)$. This expression does not of necessity imply the possibility of measuring either $A$ or $E$, neither does it imply that $A$ and $E$ are variables in any other sense than that they may or may not exist—or be observed or postulated—at particular instants. The functional relation simply implies dependency: if $A$, then $E$. As a matter of fact, however, there are very few cases in which both $A$ and $E$ (their meanings) cannot be conceived in the mathematical way. The facts and hypotheses of nature fall into series of such a character that it becomes possible to designate the individual fact or hypothesis by indicating its position in the series of which it has been made a member. Series of this sort are manufactured by selecting a number of natural factors which are more or less alike, and arranging them in order of their difference from some arbitrarily selected individual among them. Since the majority of much used scientific symbols stand for general rather than special meanings, that is, for groups of similar meanings, $A$ and $E$ may well be the symbols of generic rather than individual concepts. $A$ stands for one series of similar natural factors arranged in order of
their mutual differences, while \( \mathbb{B} \) denotes another series formed in a similar manner. In this case the functional relation has an amplified significance; it now indicates that if we select a particular member of the \( A \) series we will find along with it in nature a specific member of the \( \mathbb{B} \) series. The functional relation states that these two natural \( \mathbb{A} \) series are parallel in interdependency; given a particular exemplar of the \( A \) genus, a particular exemplar of the \( \mathbb{B} \) genus must accompany it. We may or may not be able to describe the character of this parallelism by the use of numbers; but if we succeed in doing this we add nothing to the meaning of the functional relation; we simply throw it into a form which is more convenient than that which points immediately to a qualitative interdependency. As we shall employ the formula \( A = f(\mathbb{B}) \) in this thesis—\( A \) and \( \mathbb{B} \) being any two symbols—it will imply either the simple fact that when the particular thing we call \( \mathbb{B} \) is given, that called \( A \) will be given also, or, when \( A \) and \( \mathbb{B} \) are generic terms, the fact that particular exemplars of \( A \) are always accompanied by particular exemplars of \( \mathbb{B} \), and in such a manner that all of the individual relationships may be indicated in a table made up of two parallel columns, each column containing the symbols for the members of a single genus only. When \( A \) and \( \mathbb{B} \) can be given a mathematical significance the functional relation will signify the possibility of a graphical representation of the interdependencies of the variables concerned. It is perhaps needless to say that the functional notation as here defined is not limited to the expression of the relationship existing between a pair of individual meanings, or between two genera; any number of symbols may enter, ac-
ccording to the facts. This and allied matters will receive further consideration when we come to discuss the application of mathematics to psychological phenomena.
Section VI : The Symbolic Logic of Difference.

Fundamentality of Discrimination and Comparison in Science

The indispensable instruments of scientific investigation are those of discrimination and comparison. Discrimination and comparison are mental processes of the order of perception; they are the expression in consciousness of the action of a fundamentally important cerebral mechanism which has been developed in the course of the struggle of the organism for its existence. The ability to "recognize" differences and similarities is the basis of all nervous or reactional development. The adaptive responses of such low biological forms as the Protozoa seem always to depend upon a nearly pure Unterschiedempfindlichkeit, or sensibility for differences. In psychological studies, in which the method is purely introspectional, the sensibility for differences is even more important than in common life or in physical science, for here we very often lack that factor of perception which has developed to such a high degree in the reaction of the human mechanism with its environment: the sensibility to specific positions and spatial magnitudes.

Nature and Meaning of Discrimination, and Comparison...

The method of argument which will be employed in the discussion of psychological questions in this thesis will be based upon certain assumptions and conventions with reference to the nature, meaning and mode of expressing the results of discrimination and comparison. In the first place it will be assumed that difference and similarity are not only perceptual

1 JENNINGS, H. S.: Contributions to the Study of the Behaviour of Lower Organisms; (1904).
but are also factual. Two existences wholly out of relation with any discriminating and comparing psychosis would still be similar or different, and, moreover, to a definite degree, so that discrimination and comparison in themselves add nothing to the facts which they consider; they are merely the mechanism whereby the facts get themselves expressed. For all the purposes of this thesis, comparison may be described as the appearance of the word "similar" in a consciousness in which that word finds its meaning in certain other components of the consciousness which are said to be compared, while discrimination is, analogously, described in the use of the word "different."

It will be assumed in this thesis that our ability to perceive differences in difference, and similarities in difference is also dependent upon the mode of existence of the factors to which discrimination and comparison are applied.

The Symbolism of Difference...... In order to reduce the amount of space required in the discussion of these relations we shall make use of a symbolic method which may be described as follows. If A and A' are the symbols which have as their meanings two qualitatively concrete psychological facts, the difference between these facts will be denoted by the convention: (A - A'). If the difference between A and A' is slight, so that they can be regarded as two members of the same genus (cf. page 67), we may employ the notation ΔA, so that (A - A') = ΔA, where the sign = always signifies that the symbol on the one hand has the same meaning as that on the other hand. Equations such as the above need not be thought of as mathematical, although they are of the same general character as mathematical equations. A and A' have qualitative meanings, and the express-
ions \((A - A')\) and \(\Delta A\) denote the difference in quality which we are able to perceive in discriminating between them. Whenever in the course of this thesis we employ capital letters in symbolic expressions of this sort, the meanings may be regarded as qualitative in character, while when we make use of small letters (lower case) the meanings are to be regarded as quantitatively determined. The distinction between these two points of view, while superficial, is quite important.

When two (qualitative and concrete) psychological facts, \(A\) and \(A'\), are perceived to be exactly similar we shall write \((A - A') = 0\), which indicates that there is no difference between them, that they cannot be discriminated. The transformation to \(A = A'\) is legitimate since this expression merely signifies that \(A\) and \(A'\) have the same meaning, which is the case if the meanings of \(A\) and \(A'\) cannot be discriminated. Equations of this sort of course involve the neglect of some ideational variable such as time or position, which in the first instance gave us two facts to be compared. These may be safely neglected when we are not interested in them, or in their consequences; when they do not affect our discussion in one way or another. Expressions such as \((A - A')\) in parentheses should not be confused with expressions of the type \(A - \overline{A}\), out of parentheses (cf. page 65). There are certain cases in which the parentheses may be removed without alteration of the meaning, but this is not generally true.

In an exactly analogous manner we may express the difference observable in discriminating between two differences, by an expression of the type: \((\Delta A - \Delta'A) = \Delta^2A\), the meaning of the expression to be re-
garded as wholly qualitative in nature, and as involving only qualitative discrimination. Of course, if $\Delta A$ and $\Delta' A$ are the same, we have: $(\Delta A - \Delta' A) = 0$, or $\Delta A = \Delta' A$.

Opposite Differences......    In using such a symbol as $\Delta A$ we imply some initial factor $A$, with which we compare another factor $A'$. We say in the first place that the difference between $A$ and $A'$ is $(A - A') = \Delta A$. Now suppose that we permit $A'$ to vary. This variation may be of one of three sorts. It may be a variation of such a character that $A'$ will become increasingly like $A$, or, on the other hand, it may be such that $A'$ will become increasingly unlike $A$. The third possibility is that the degree of difference or similarity between the two factors will remain unchanged. The entrance of this quantitative conception, of greater and less difference, enables us to define two types of differentiation, the qualitative and the quantitative. Both are at bottom qualitative, but one of them arouses the perception of more-less while the other does not.

Neglecting for the time being at least the qualitative difference (so defined), let us say that a variation which makes $A'$ increasingly like $A$ is opposite to one which makes it increasing-ly unlike it, and let us indicate this sort of opposition by the use of the signs $+$ and $-$. Then if $A'$ changes so as to become exactly similar to $A$ the change is $\Delta A$, but if it changes so as to become more different, we may denote the change by $- \Delta' A$. But suppose that, instead of $A'$ changing to $A$, $A$ changes to $A'$. Then the change will be exactly the same as in the first instance—for the same difference will be abolished—but it will be opposite, and may be written as $- \Delta A$. These considerations lead us to the following statement, which is in part a definition: The
difference between \( A \) and \( A' \) is the same as that between \( A' \) and \( A \), except that it is opposite. Symbolically, we write: 
\[
(A - A') = \Delta A, \quad (A' - A) = -\Delta A.
\]

An extension of this line of reasoning may prove useful. Suppose that we transform the equation \((A' - A) = \Delta A\), so that it becomes: 
\[
(A' + \Delta A) = A.
\]
This amounts to a definition of the plus sign within a parenthesis. In the sense in which we employ the word in this context, the sum of any meaning and its difference with respect to another meaning is the same as that other meaning. In other words, adding a difference symbol \((\Delta A)\) is equivalent to substituting the word for that with respect to which difference is observed or postulated.
Section VII: The Relation Between Quantitative and Qualitative Symbolism.

It is necessary to say a few words concerning the relation which holds between purely qualitative and quantitative symbolism. The ruling concept of mathematical thought, that of quantity, finds its basis in a specific perception, a perception which is wholly analogous in fundamentality with those of similarity and difference (cf. page 70), and which we shall call the perception of more-less. This is actually a development from the simple discrimination reaction of consciousness; it is a discrimination which embodies the fundamentals of classificatory method.

Series of more-less arrange the factors of our experience and of our conception into series (cf. page 67). These series are formed in the following way. A large number of factors (meanings) which show markedly resemblances to one another are selected. A single one of these is arbitrarily chosen and the rest are arranged with respect to it in such a manner that the difference between every member of the series and its neighbor is as small as possible. The production of an arrangement of this sort of course depends upon the perception of more-less, which makes it possible for the mind to recognize larger and smaller differences. A series of this sort we shall call a series of more-less. It is to be regarded, generally, as conceptual in form; it is a thought structure. But if need be, a more-less series may be made concrete either by arranging the actual factors concerned, in space or time, or by constructing a spatial or chronological
schema of the series by use of the symbols for the factors. An example of the former may be found in the so-called color pyramid of psychology, or in the graduated meter stick of physics; an example of the latter appears in a table of specific gravities, numerically arranged. In the development of the applications of the more-less percept, or the concept of quantity to experience the first factors to be considered were groups of "things"; the symbols for groups of "things" are numbers, and a schema of a more-less series of such groups is given in the consecutive series of numerals: 1, 2, 3, 4, 5, 6, etc.

Dimensions

When we attempt to construct a series according to the rule that the sum of the differences observable between every member and its neighbor shall be a minimum, we often find that this series will be of such a character that if it were represented or realized in space, it would be continuous in more than one direction. This fact gives us the basis for the conception of the dimensions of any more-less series. The series of groups of "things", the number series, mentioned above, is a one-dimensional series; the series constructed from the material of visual sensation, on the other hand, is a three-dimensional series. So, also, is that necessitated in Euclidean geometry. Any conceivable number of dimensions may, however, be necessary, in different cases. Dimensionality rests, at bottom, upon the facts already indicated (cf. page 73), that differentiation may be of three general sorts; that which increases a difference, that which decreases it, and that which does not affect it quantitatively at all. If in the relation $(A - A') = \Delta A$, $A'$ changes in such a way that $\Delta A$ alters--as it must--but does not alter quantitatively, $A'$ is changing in a
new dimension, where the old dimension is that determined by increase or decrease observable in $\Delta A$. If, changing in this new dimension, $A'$ passes into $A''$, we may write $(A' - A'') = \Delta A'$, and the qualitative difference between $\Delta A$ and $\Delta A'$, $(\Delta A - \Delta A')$, is the difference between the two dimensions. One usually states that the number of dimensions in which any meaning is capable of varying is determined by the number of attributes it exhibits, but the converse of this assertion contains more truth. The conception of dimensionality does not depend for its existence upon recognition of the dimensions of space, any more than the conception of quantity depends upon the recognition of spatial magnitudes. It happens that spatial dimensions and magnitudes are those which are easiest to study and to think about, for the reason that in the evolution of the human mind the struggle for existence has forced the development of space perceptions and discriminations to excess. Variation along any dimension is not necessarily unlimited in its scope, and it is not of necessity wholly independent of variation along other dimensions; dimensionality may be a matter of more-less. In fact it is doubtful if any variation of $A'$ whatsoever is possible in which $\Delta A$ will not exhibit some quantitative change, however slight.

Number and the Quantitative Symbolism. When we come to the construction of such more-less series as that given in the color-pyramid, we have already before us the striking precedent of the numerical series. Now each more-less series is made up of many concrete and qualitative factors (the factors arranged into the series), and if we chose we could continue to represent each one of these factors by the same qualitative symbol which stood for it previous to the formation of
the series. However a more convenient method of representation (symbolization) suggests itself. This consists in an adaptation of the numerical symbols to fit the general case. We may discard all of the original qualitative symbols except one, and in their place we may substitute numbers, one number for each factor in the series, the more-lesser arrangement being retained both with respect to the order of the numbers and the order of the members of the series. The one qualitative symbol which we retain represents the point of departure of our series; the numbers, when given, stand for successively greater degrees of difference exhibited by the members of the series when they are compared with the meaning of this single qualitative symbol, which thus becomes representative of the quality of the entire series.

Since number was invented to designate the properties of a onedimensional series (cf. page 78) we must retain a special qualitative symbol for every dimension possible or actual in the series we are considering. The qualitative symbols thus retained come, therefore, to stand for the attributes of the individual members; numbers attached to these qualitative symbols indicate the degree in which these attributes are exhibited by the particular member of the series which is specified. If $A$ is the qualitative symbol for a particular fact in nature, and this fact possesses, or exhibits, the attributes $X$, $Y$ and $Z$, and if, moreover, the meaning of $A$ is a member of a series, all of the members of which possess the same attributes, provided we have selected some one member as a point of reference, we can fully describe $A$ by numbers having reference to these attributes. In our discussion of the facts of visual sensitivity, we shall designate numerical values of this sort by use of lower case (small) letters corresponding with the
upper case (capital) letters which are employed as qualitative symbols. Thus in the above case \( A \) would be described quantitatively by the numbers \( \bar{x}, \bar{y}, \), and \( \bar{z} \). The relation which we conceive to be the qualitative equivalent of the relation which we observe between the quantities \( x, y, \) and \( z \) above, may have a relation to the symbols \( \bar{x}, \bar{y}, \) and \( \bar{z} \) which is analogous with that which appears between a measure and the unit in terms of which it is a measure. In order that we should come to a thorough understanding of the meaning of this analogy—which at bottom is much more than an analogy—it would be necessary to consider in detail the problem of the numerical representation of sections of a continuous series. This problem is a grave one, and arises from the fact that number is intended in the first instance as a symbolism of discontinuous quantity (as given in groups of "things"), while almost every other quantitative series turns out to be continuous. We solve the problem wherever possible by selecting a unit and by the use of this unit we divide the continuum of the series into a number of segments, which we then designate as we formerly designated the groups of "things", by the use of numerals. A unit may be defined as an arbitrary but constant difference along the dimensions of the series within which it is a unit. When the members of a series are determined by use of the concept of a unit, the differences existing between any member of the series and its neighbor in a single dimension are constant or equal. In psychological measurements, an attempt is made to secure this equality of difference between the different numbered members of a series, by use of the measurement method of difference limen, on the assumption that the least perceptible difference in any
The relation which we conceive to hold between the quantitative and the qualitative symbolism must now be given brief exposition. In the first place we may state the general principle that every symbolic relationship which can be expressed in qualitative symbols can also be expressed in quantitative symbols, when these are available, provided that the dimensions of both sides of the equation are the same. Thus, if \( A = A_1 + A_2 + A_3 \), we can write \( a = a_1 + a_2 + a_3 \). But if \( A = A_1 + A_2 + \bar{E}_1 + \bar{E}_2 \), we cannot write \( a = a_1 + a_2 + \bar{E}_1 + \bar{E}_2 \), since this involves a dimensional inequality; a shift of units. However, if \( A = f(E) \), we have \( a = f(E) \), since here the form \( f( ) \) explicitly cancels the dimensions of both sides, or makes them equal, as we chose to regard the matter. Relations of difference when in a single dimension will also obviously go over from the qualitative to the quantitative form. If \( (A - A') = \Delta A \neq (A_1 - A_2) \), we can write: \( (a - a') = \Delta a = (a_1 - a_2) \). This is not a valid transformation for a difference the quality of which is polydimensional; it holds for but one attribute. Other relations of this general character will be spoken of as they appear in the course of our argument.
PART THREE: THE PROPERTIES OF THE ELEMENTARY VISUAL SENSATION.

Section VIII: Some Preliminary Remarks Concerning

The Visual Consciousness.

The Visual Consciousness
the Starting-point of . .
the Theory of Visual Sensitivity.............

In the attempt to develop
the science of visual sensitivity
one may conceivably start with any
of the phenomena included with the department of nature which
has been selected as the subject-matter of the science in ques-
tion, and, after completing the analysis and a description of
the forms of combination of the elements of these phenomena,
one may proceed to an investigation of the possible ways in
which these descriptions may be correlated with other phenomena
in the same department of nature and with the laws describing
natural processes in general. We may conceivably begin our analy-
sis of the department of visual sensitivity at any point and
then develop the theory of the subject by excursions thence
into other regions. But when we are required to decide what
point we shall indeed select, we experience little hesitation
in settling upon the subjective—that is, the psychical—pheno-
mena, and in particular upon the elementary visual sensation,
as the most promising region in which to begin our attack. The
reason for this decision lies in the fact that all of the phenome-
na of vision are correlated with or are constituted by means
of the elementary visual sensations; these sensations have the
broadest possible connection with the entire department of vis-
ual sensitivity, because they lie at the focus of the whole
visual process, are, in fact, its raison d'être. Hence if we
study them at the outset we shall find ourselves acquainted with the central facts of our special department of nature, and these facts, like sign-posts upon streets leading radially outward from the market-place of a city, will direct us to all of the outlying regions.

We have asserted in another section that the business of science is the analysis of experience, followed by the formulation of the modes of combination of these elements. This implies that experience presents two separable aspects, those of substance and of structure. The substance of experience is the sum of the results of the analysis of experience. The structure of experience is the manner in which we find these elementary factors combined. Now the elements of experience are of but two general sorts, sensation and affection. We are not here concerned with the latter, and for the purpose of our argument we may assume that the visual consciousness has but one general type of elementary factor: the visual sensation.

The forms of combination in which the elementary sensations which constitute the substance of experience, are found, differ in the various departments of consciousness. We may speak of the structure of any consciousness as its ideation, and in this way we must describe the typical ideation of the naive visual consciousness as that of three dimensional space. The science of geometry is simply a development and description of the properties of this sort of ideation. But just as in the particular inquiry which we are now pursuing it is feasible to neglect the substantial element of affection which exists in the visual
as in other forms of consciousness, so it is possible for us
to neglect one of the three dimensions which characterize the
typical ideation of the visual consciousness. The dimension
which from our point of view is negligible is that of depth,
and we are able to leave this dimension out of consideration
because the results of general psycho-physical investigation
show that it is not intimately dependent upon the fundamental
conditions of visual sensitivity. From the standpoint of the
theory of visual sensitivity, then, the ideation of the visual
consciousness may be regarded as two dimensional (space), the
space described in plane geometry.

The Visual Field..... When we make a special study of all of
the ideations which are presented in any parti-
cular department of experience we find that they present many
peculiarities in common, and that descriptions of one may be
transformed into descriptions of another by special logical
processes. The common properties in ideation presented by the
varying perceptions which make up any specific department of
consciousness may be described as the ideational field of that
department. The ideational field of the department of visual
consciousness we shall speak of as the field of vision, or as
the visual field, or simply as the field, the symbol for which
is F.

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Section IX : The Attributes of the Elementary Visual Sensation.

Definition of the Elementary Visual Sensation, S....

Because we have defined sensation as the non-ideational, substantial or existential aspect of a consciousness it does not follow that sensation in the concrete—and an element of existence must certainly be concrete—can actually be freed from the ideational context. It is very desirable, however, that it be freed from this context in our conceptions. In order that we may speak of visual sensation without implying any special ideational conditions it is necessary to adopt certain conventions. Every concrete instance of visual sensation is also a concrete instance of visual ideation. We never experience either a purely ideational or a purely sensational consciousness. In general any concrete visual sensation will present both special form and special position in the visual field. But if we define the elementary visual sensation as a sensation the area of which is that of a point, we shall have eliminated the ideational attribute of extensity, and have only to consider that of position. The position of a point in a two dimensional manifold may be completely represented by two variables, so that we may adequately describe the concrete elementary visual sensation by the use of three independently variable terms, \( \theta \), \( d \), and \( S \), in which \( \theta \) and \( d \) are ideational factors denoting the position of the point sensation in the first and second dimensions respectively, and \( S \) has as a meaning the entire substantial or abstract non-ideational character of the sensation. It may be objected that a point sensation cannot be concrete, because a sensation having no area, no
extensity, has no existence. This is, of course, true in the
conceptions of the sort as such he wrote without anything
limit, but in this psychological discussion, as in analogous
cases, we must study the characteristics of the existence
physical argument, a point sensation need not be regarded as
which may appear at any point in the visual field we find that
an actually areless entity, but rather as a sensation whose
variables are not externally alike, but that they can be
area is so small that recognition of its existence would have
classified-method. The ground of taking even the existence of certain
no appreciable effect upon the results of the discussion. A
point in the visual field is simply a region small enough so
that it may be considered the first order of the generic
that its internal space relations are insignificant in compari-
son with its external relations. In general, such a point may
be defined as a region which cannot be perceived as an area; in
other words, it is the so-called physiological point, or funda-
mental determinant of visual acuity. By the term an ele-
mentary visual sensation, and its symbol, S, let us, then, com-
ppletely describe existences in any point of the visual field,
the point in question being defined by the two quantities \( \theta \) and
d. The exact manner in which \( \theta \) and d are to be measured need
not trouble us at this stage of the discussion, since it is
clear that two variables can always be selected which when made
determinate will completely describe any specific point in the
visual field. The symbol, S, is subject to the limitation al-
ready imposed upon it on page 62. When we speak of the ele-
mentary visual sensation we employ the term as a genus name,
or as a variable which must become determinate in any concrete
case. S may be employed in a similar manner.

The Problem of the Attri-
butive Analysis of S.....

The problem which we now con-
front may be described as that of
the attributive analysis of the elementary visual sensation S.

Now a veritable decomposition of S is beyond the question, for
it has been defined as the final existential term in the visual
of consciousness, and cannot as such be broken up into anything simpler. But when we study the characteristics of the existences which may appear at any point in the visual field we find that these existences are not uniformly alike, but that they can be classified—thrown into groups—by taking cognizance of certain more or less constant types of variation which they exhibit. In other words, we discover, in the first place that $S$ is a generic rather than an individualistic conception, and that within the genus $S$, there are a certain definite number of varieties: $S', S'', S'''$, etc., and that these varieties may be grouped into species: $S_1, S_2, S_3$, etc., by taking advantage of the degrees of similarity or difference observable between the varieties.

We may describe the state of existence which permits us to discriminate between one exemplification of the variable $S$ and another—between $S'$ and $S''$, or $S_1$ and $S_2$—as an attribute of $S$.

We have already indicated the general nature of attributes in discussing the elements of symbolic logic (cf. pages 73 and 76). It is clear that so far as $S'$ and $S''$ are indistinguishable one from the other, they exhibit the same attribute or attributes, but that so far as they are discriminable they exhibit different attributes, provided that, in the first stance, we say nothing concerning the relative degrees in which these attributes are possessed. If all exemplifications of $S$ were alike we could in no way determine the number of attributes possibly possessed by it; the conception of attributes arises only in the processes of comparison and discrimination. In order that the number and character of the attributes be discovered we must take a multitude of exemplars of $S$, arrange these exemplars into a series
of more-less, and ascertain the dimensions of the manifold thus produced (cf. page 77).

Attributive Analysis Demands no Complexity.... The simplicity of a sensation is thus in no way dependent upon the number of attributes it may be capable of exhibiting; a sensation capable of exhibiting a hundred attributes would be exactly as simple in the purely analytical sense of the word (that of introspective analysis) as one capable of exhibiting only a single attribute; a point which can move in three or in n dimensions is not different in itself from one which cannot move at all. An attribute is simply a generalized dimensionality of the conditions limiting the existential character of any sensation or image. If a sensation is permitted to vary in n independent ways, it is said to exhibit--or, to avoid monotony of expression, to possess--n attributes. In special cases the degree in which particular ones among these attributes are exhibited may chance to be zero; this is a natural outcome of the selection of a specific point of departure for the measurement of attributive degrees (cf. page 78).

Modal Points in the S More-less Series. Now observation shows that the visual sensation, S, exhibits six more or less independent attributes (cf. page 77). If we compare all possible states of S we find that the genus S splits into six species. It is true that these species are not separated from each other by rigid lines of demarcation, but such a separation is seldom possible in any field of classification; the occupants of any department of nature are connected with each other by bonds of similarity which are many and strong. What we find is that if we arrange a large number of exemplars of S--taken so as to
yield the greatest possible variety—in order of their similarities and differences, we find that as we pass along the series from one end to the other we come into certain regions within which the differences which are observed are of a uniform character. Upon reaching the end of one of these regions the manner of differing changes quite abruptly, continues for a time and then alters again. If we denominate these parts of a series regions of similar change, we may further define such regions as those in which the sensation differential, $\Delta S$, is of constant quality. This implies that at the end of any region of similar change, $\Delta S$ varies in quality, and becomes, say, $\Delta' S$. Let us speak of the point in a series in which a change in the sensation differential occurs as a modal point.

Further observation shows that any $\Delta S$ thus defined is itself attributively complex. If we move in either direction from a modal point we find that the change which occurs is similar and also different. When we compare the change which takes place in moving to the left from any modal point with the change which takes place in moving to the right we find that we are obliged to apply to the two both the judgment of similar and the judgment of different. This similarity and difference is, of course, qualitative. The paradox can be cleared up if we decide to regard the sensation differential by the use of which we describe the change which is observed in passing from one member of a sensation series to another as in itself complex. We have said above that there are certain points in the $S$ series at which $\Delta S$ may be said to change to $\Delta' S$. Now let us define two new differentials in such a way that
(ΔH₁ - ΔH₂) = ΔS; and \(\Delta H_3 - \Delta H_1\) = Δ'S. Then in passing from the modal point in one direction we have Δ'S = (ΔH₃ - ΔH₁), and passing from the same modal point in the opposite direction (cf. page 73) we have -ΔS = -(ΔH₁ - ΔH₂) = (-ΔH₁ + ΔH₂). In the sensation differential involved in each of these changes we have the similar element - ΔH₁', which resumes our judgment and perception of similarity in change, while we also have the different elements, +ΔH₂ and +ΔH₃, which resume our judgment and perception of difference.

The Color Pyramid. We have spoken of the arrangement of the many different samples of S, above, as if in the attempt to form a series which should present a minimum degree of difference between contiguous elements, as if such a series were monodimensional, or linear in character (cf. page 76). Experiment shows, however, that if the choice of exemplars of the genus visual sensation is broad, the arrangement must be made tridimensional. The so-called color-pyramid is the construction most perfectly fulfilling the requirements of the case.

Changes of the Sensation Differential Along the Equator of the Color-pyramid. If for the moment we confine our attention to the quadrangular equator of the pyramid, we may consider some of the possible results of the above discussion. The modal points spoken of above are upon the equator—four in number—and are placed at the four angles of the equator. At each one of these points we have a change in the sensation differential of such a nature that one of its two constituents drops out, or becomes zero (nothing); the other changes sign and a new one appears. If as we approach one angle of the equator the differential has the constitution: \(-ΔH_4 + ΔH_1\), upon reaching the angle
it becomes for the moment = 0, (cf. page 66) since $\Delta H_4$ becomes zero, and $\Delta H_1$ changes sign. Upon passing this modal point the constitution of the differential becomes $(-\Delta H_1 + \Delta H_2)$, which obtains until the second corner is reached, when the differential again becomes momentarily equal to nothing, and subsequently we have $\Delta S = (-\Delta H_2 + \Delta H_3)$. At the final mode, the differential changes to become $(-\Delta H_4 + \Delta H_1)$, as at first.

Consequences of this Argument in Quantitative Form. Now by throwing these differential terms over into quantitative form, we may arrive at a very interesting result. It will be noted that at each modal point a certain $\Delta H_n$ disappears—is equal to zero, has no meaning—and that in passing through that point it sign changes from plus to minus, no matter in which direction we happen to be moving. Now this is exactly the condition for a maximum of $K_n$, if we find it possible to interpret $\Delta H$ and $H$ quantitatively, and to adopt the method of reasoning of the differential calculus. It has been stated that the symbols $H$, $S$, etc., stand for qualitative rather than quantitative meanings. But it has also been asserted that the distinction between the quantitative and the qualitative is not fundamental, that the quantitative symbol is merely a special device for indicating a really qualitative meaning. The relationships which exist between quantitative and qualitative symbolism have already been considered to some extent (cf. page 80). Let us here investigate these relationships as they are exemplified in the mutations of the sensation differential. When we defined "regions of similar change" and affirmed that in passing from one point to another of such a region the sensation differential, $\Delta S$, did not alter in quality, we admitted that the differences existing
between one part of the region and another were capable of mathematical description, for the only prerequisite of a mathematical description is that we possess a unit of measurement which is substantially the same for the whole range of meaning to which it is to be applied. Let us define the smallest perceptible difference in S in any region of similar change as the unit of difference in this region. If this unit is $\delta s$, we may write: $\delta s = (-\delta h_4 + \delta h_1)$. At the first modal point $\delta s$ changes to $\delta's$. This means, in part, a shift of units of measurement (a change of dimensions; cf. page 30), but since $\delta's = (-\delta h_1 + \delta h_2)$, at the modal point $\delta h_1$ changes to $-\delta h_1$, passing through zero, so that we may write, for that point, $\delta h_1 = 0$, or $h_1 = a maximum$. Similarly, at the second modal point, $h_2 = a maximum$, at the third, $h_3 = a maximum$, and at the fourth, $h_4 = a maximum$. The psychological meaning of these facts is obvious. The value of $h_1$ at any point upon the equator of the pyramid is a measure—to the first order of approximation, at least—of the degree in which the sensation situated at this point resembles the sensation at the modal point, $H_1$; $h_1$ is a maximum at this point because, of course, any sensation resembles itself more than it does any other sensation. This, naturally, would apply to sensations situated at any point upon the equator, but examination of our argument will show that the psychological instruments of discrimination and comparison will in no wise permit us to select any points other than those at the vertices of the base of the pyramid as modal.

Definition of the Hues.....

The quantities: $h_1$, $h_2$, $h_3$, $h_4$, are, of course, degrees of redness, yellowness, greenness, and blueness, respectively, and hereafter, we shall substitute for them the symbols: $r$, $y$, $g$, and $b$, so that: $h_1 = r$, 
h_2 = y, \ h_3 = g, \text{ and } \ h_4 = b. \text{ The corresponding qualitative terms: red, yellow, green and blue, may be symbolized by, } R, \ Y, \ G, \text{ and } B, \text{ respectively. We shall speak of the qualities as the hues. The hue of a sensation, on the other hand, will be the numerical value of } r, \ y, \ g \text{ or } b, \text{ or that sensation, its position, in other words, upon the equator of the color-pyramid.}

Tint and Chroma... the hues, and turn to a consideration of the other two dimensions of the color pyramid. It is found that any sensation may vary with respect to its neighbor without moving either towards it or away from it, upon the equator of the pyramid; but by moving towards the axis. The interval between any equatorial point and the axis itself marks a region of similar change (cf. page 89), but the axis itself marks a modal point. If we designate the sensation differential by \( \Delta S \), as before, in passing through the axial point the sense of the differentiation changes to \( \Delta' S \). We recognize, however, that in moving in either direction from the axial point there is an element of similarity as well as of difference in the resulting change, so that we write: \( \Delta S = (\Delta T - \Delta H_c) \) and \( \Delta' S = (\Delta H_a - \Delta T) \). Reasoning as before, we have, in mathematical notation, at the axis \( \delta t = 0 \), or \( t = a \text{ maximum. We shall speak of } t \text{ as the tint of the sensation, } S. \text{ Since the validity of this argument is not dependent upon the specific point in the equator at which we start to move towards the axis, what we say of the pair of hues, } H_c \text{ and } H_a, \text{ will be true for any similarly relation pair. As } t \text{ approaches a maximum the value } h_c \text{ or } h_a \text{ approaches zero, for at the axis:}

\[ (-\delta t - \delta h_c) = (\delta h_a - \delta t) = 0. \text{ On one side of the axis } h_a \text{ is } 0, \text{ while on the other } h_c = 0. \text{ We may, then, define a generalized} \]
variable, $h$, which applies to any sensation $S$, and is a measure, so to speak, of the hue ness of the sensation. This hue ness or, as we shall call it, chroma, of the sensation is obviously a function of the difference between $t$ and some constant, for when $t$ attains a certain value, $h$ becomes zero; the sensation has no chroma. It is, of course, not certain that the relation between tint and chroma is the same for all hues; the so-called constant may itself be a function of $r$, $g$, $y$, and $b$.

Black and White.... We have still to consider the third dimension. If we start from any point in the pyramid, and move so as to have a component of motion parallel to the axis, the change corresponding to this component in the sensation is found to consist in an alteration of the quality of the tint, $T$, of the sensation. This is not—so far as $t$ is concerned—a quantitative change; it is—rather—a modification of the units in which $t$ has to be measured. If we indicate the sensation differential describing change along the third dimension of the pyramid, by $\Delta S$, as before, we find that this variable has no modal point. It permits a variation of the sensation between two limits, between which the sense of differentiation is constant. If we define $\Delta S$, in this instance, as $\Delta W$, when differentiation is thought of as taking place from the region of the equator towards the upper pole of the pyramid, the corresponding quantity, $w$, the whiteness of the sensation, will have a definite value $w_m$, when the variation in the direction of the upper pole of the pyramid is maximal. A variation in the opposite direction will be described in terms of $-\Delta W$, and will be $\Delta B$, if we define $\Delta B = -\Delta W$, so that we have, at the lower pole of the pyramid: $b = b_m$, a definite maximal measure of blackness. Thus any
specific whiteness measurement can always be represented as a function, \( w = b_m - b \), of the blackness measure; perfect blackness is defined as zero whiteness, and vice versa.

Luminosity. It should be noted that the whiteness or blackness of any visual sensation does not vary independently of its tint. If a sensation has no tint \( (t = 0) \), that is, if the chroma is perfect \( (h = \text{a maximum}) \), it cannot vary at all in the axial dimension. This fact is represented in the color-pyramid by its tapering form. Sensations possessing perfect chroma are represented about the equator. If they move in the third dimension without moving in the second at the same time they fall outside the volume of the pyramid, that is, they cease to exist, are not sensations which are of a possible variety. We have stated above that the sensory modifiability which is represented by the axial dimension of the pyramid means simply a change in the units in which the tint \( (t) \) is measured. This being the case, we can define a quantity, \( tw \), which will be characteristic of every sensation. This we shall call the luminosity of the sensation; it is a measure of the whiteness alone, as opposed to the whiteness or blackness—the tint—of S.

Attributes and Their Schematic Relations——The variables \( r, g, b, y, b, \) and \( w \), we shall regard as measures of the degrees in which the fundamental attributes, \( R, G, B, Y, E, \) and \( W \), respectively are exhibited by any elementary visual sensation, \( S \). We shall distinguish between fundamental and derived attributes; the latter are those of tint, \( (T, t) \); luminosity \( (tw) \), and chroma \( (h) \). The derived attributes are quantitative only, except in the case of the tint, in which \( T \) stands for the combined fundamental attributes of \( W \) and \( B \) in
S, T = W + E. These derived and fundamental attributes will be regarded as components of the quality of the sensation. Different S's exhibit these attributes in different degrees, but no S exhibits all of them. A study of the color-pyramid will reveal the relations which exist between these various attributes. Since the order of modal points with respect to hues is inevitably cyclic, and of the form \( \begin{array}{c} R \\ B \\ G \\ Y \end{array} \), we are able at once to write the relations: If \( g > 0 \), \( r = 0 \), or \( y > 0 \), \( b = 0 \), and conversely: If \( r > 0 \), \( g = 0 \), or \( y > 0 \), \( b = 0 \). In other words, the hues R and G, and Y and B, are mutually exclusive. The hypotheses of Hering and Ebbinghaus have been styled theories of antagonistic colors, and an attempt has been made to classify doctrines with regard to the nature of color sensation by the use of the criterion of color antagonism. But it is obvious that a purely empirical formulation of the facts with regard to the distribution of the attributes of visual sensation makes the hues R and G, and Y and B antagonistic; whenever we experience one member of these pairs we fail to experience the other at all. From the above observation and the cyclic nature of the hue series there follows the rule that any hue may coexist with either of two other hues—those contiguous with it in the cycle of hues—but not with both simultaneously. It should also be remarked that in a relative sense all of the hues are antagonistic. Even those hues which—so to speak—fuse with each other are observed to be present as attributes of the sensation in reciprocal degrees, so that in a sensation whose hue contains, for example, the constituents Y and G, the relation \( g = k - y \) obtains, where \( k \) is a con-
stant, for constant chroma. The greener the sensation, the less yellow it is. This relation is obviously implicit in the constitution of the color-pyramid, as are seven others of a similar character, basic. We have already noted the relation which obtains between the chroma and the tint of the sensation; these, like the antagonistic hues mentioned above, vary reciprocally; high chroma means low tint, and vice versa. A similar relation exists between the blackness and the whiteness of the sensation; this has already been formulated (cf. Page 95).

Synopsis of Our Analysis. We may, on the basis of the above attributive analysis, give the following description of any visual sensation, S. The most prominent attribute of visual sensation is tint. Certain specimens of S possess a maximum tint, and consequently zero chroma. The attributive constitution of such sensations may indicated as $S = T = [w \times W, (b_m - w) \times B]$. In other specimens of S we discover an attributive replacement of tint by chroma, so that the attributive composition of the sensation becomes: $S = T, H = i \times \left[ t \times \left\{ w \times W, (b_m - w) \times B \right\}, h \times (r \times R, g \times G, b \times B, y \times Y) \right]_{\theta \partial}$ in which $r$ and $y$ are zero if $g$ and $b$ are real, and in which $r = k - y = k' - b$, etc. The method of symbolism: $w \times W$ merely indicates that if $w = 0$, the attribute $W$ is not exhibited; the equation is not quantitative but qualitative. Theoretically it is possible to have a sensation which has perfect chroma and no tint, since $t = \text{const.} - h$, but in point of fact no such sensation is ever experienced. The quantitative factor $i$ is the intensity of the sensation, and it may be interpreted as the degree of existence of $S$, or as the degree in which $S$ is in consciousness. In addition to the above intrinsic attributes of $S$, the two ideational attributes, $\theta$ and $d$, which
constitute the position of S in the field, should not be forgotten.

Meaning of the Color-Pyramid. The above discussion has been carried on from a purely psychological point of view.

The color-pyramid is a psychological construction; it has nothing at all to do with the physical or visible spectrum, with degrees of illumination, purity of lights or other physical or perceptual factors. If we should attempt to realize the color-pyramid in actual perception we should, of course, be forced to take advantage of physical substances and processes, but even in so doing we should in no way be obliged to regard the perception itself—however caused—in other than a psychological way. As a matter of fact, however, a concrete color diagram is not essential in the perception of the relations formulated above, any more than concrete lines, angles and solids are necessary in geometrical reasoning. The geometrical way of representing the attributive relations observable between different examples of the elementary visual sensation is simply a convenient aid to the imagination.
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Definition of \( \theta \) and \( d \). We have described above the characteristics of an elementary visual sensation, i.e. a sensation of negligible area situated at any point in the visual field. Our description has been of the most general type, and now requires some modification. It has been assumed that the quality of a sensation is independent of its position in the visual field. This does not appear to be entirely true. It is found that in peripheral regions of the field certain of the hues are seldom experienced. We have said that the position of any elementary visual sensation can be adequately described for the purpose of the theory of visual sensitivity by the use of two independent variables, \( \theta \) and \( d \). These variables may now be defined as follows: The visual field is characterized by its possession of a definite point of reference known as the fixation point and located in the center of the field (approximately). If we take this point as an origin of polar coordinates, we can describe any position in the field by a distance and an angle, the angle being that made by a line drawn through the position in question and the fixation point with a horizontal line through the latter, and the distance being that measured from the fixation point to the position which is to be described. These two measures are to be denoted by \( \theta \) and \( d \) respectively. The exact units in which \( d \) is expressed are not at present of particular moment.

The possible attribute constitutions of S symbolically indicated in the preceding section (page 97) hold for any part of the visual field. But the relative number of elementary sensations exhibiting the different hues is by no means independent of the position. When d is small, or equal to zero the variety of hue presented is at a maximum. At a certain larger value the hues \( R \) and \( G \) fall off, and beyond this value are seldom experienced, while at a still greater value the hues \( Y \) and \( B \) also tend to disappear from the list of attributes of S. The exact meaning of this functional relation which appears to exist between the frequency of occurrence of the different hues and the distance of S from the fixation point cannot be pointed out until we come to consider the psychophysics of visual sensation. It may be noted, however, that if we represent the frequency of occurrence of each hue as a function of \( d \), the functions for \( R \) and \( G \) are the same, as are those for \( Y \) and \( B \). These pairs, it will be observed, are the so-called antagonistic colors.

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In our actual visual experience the modifications of the visual field are seldom of the order of the elementary visual sensation; they are constituted, rather, by a large number of S's in juxtaposition. Such a modification—in the concrete—will be spoken of as an image, I. (not to be confused with I, the visual impulse). An image may be described in terms of all of its component elementary sensations, and in terms of their positions. The latter part of the description determines the ideation of the image (cf. page 82). By the term image we denote any definite area of the visual field, with its included sensory qualities, but in general we shall speak only of images which are homogeneous in point of sensory quality.

Our every-day visual experience is made up of images—in the broader psychological sense, perceptions—which are subject to changes in position in the visual field in exact correlation with the kinaesthetic sensations which are the substance of our perceptions of ocular and bodily movement. But under certain conditions, particularly when an image is extreme in chroma or luminosity, it is followed by an image of identical ideation which fails to move in the field in synchronism with the kinaesthetic modifications, and which, moreover, possesses certain characteristic sensational attributes and undergoes certain characteristic changes in sensory quality. Images of this sort, which are fixed in the field, we call after-images. Images which move in synchronism with the bodily and ocular kinaesthesia may be denominated primary images. We may define
the following types of after-image: (1) the positive after-image, which is of the same, or similar, quality as the primary image; (2) the negative after-image, which is characterized by hues antagonistic to those of the primary image, or which exhibit a reciprocal tint; and (3) the heterochromatic after-image, the quality of which bears no obvious relationship with the quality of the primary image. The study of after-images may be made wholly psychological, but since, for us, their meaning is to be physiological, further consideration of their nature will be postponed until we come to discuss the action of the retina.

We have now completed the discussion of what we consider to be the central facts of visual sensitivity. The remainder of the phenomena of the visual process cannot be intelligently studied from the purely psychological standpoint, since the mechanism which governs them is not that of the special cortical neurons which mediate the image and the sensation. The purely subjective study of such phenomena as after-images and contrast is exceedingly unprofitable. We begin to make advances in our understanding of these processes only when we attend to their physical causes as well as to their psychical course. For this reason we will now turn to the consideration of the psycho-physics of visual sensitivity.
PART FOUR:  THE PSYCHO-PHYSICAL QUESTION IN VISUAL RESPONSE.

Section XII   : General Psycho-physical Conceptions and Assumptions.

The Disparateness of Sensation and the Physical Mechanism of Visual Response...

It has been asserted (cf. page 58) that the psychical and the physical segments of the natural department of visual sensitivity are wholly distinct. This is true. These two groups of phenomena and conceptions, the physical and the psychical are entirely disparate; it is not a boundary that separates them but a vacuous gulf. The nature and relations of the psychical may be indicated by saying that it is an exemplifiable portion of the consciousness of the person who is concerned in any discussion of visual phenomena; it is the visual consciousness of the first person. The nature of the physical may be indicated by saying that it is made up of certain facts observable or theoretically observable to some other individual than that one whose vision is being discussed, or which may be observable to the latter as parts or processes of what he knows as his own body, or the external world. Between these two sets of facts and hypotheses there is absolutely no bond of continuity; one reduces to a mechanism, the other to a complex of sensations. The mechanics and the sensations are correlated; they can be represented as functions of each other; but they are not connected; they exhibit no point, line, surface or consciousness of fusion. In describing any concrete visual response we may mention in order the physical factors already enumerated (cf. page 59): the stimulus, the stimulation, the
impulse and the visual cerebrosis; all of these form a chain of events continuous in time, in space, and in energy relations. Concomitant with the last element is the fifth factor of visual response, that of visual sensation (or the visual consciousness, in the concrete), but this is a factor wholly out of joint with the rest; it occurs in space, but somehow not in the same space as the other events; all that we seem to be able to say is that it is dependent upon the physical series, especially upon the fourth member, but that it is not a part of that series.

The Fundamental Assumption of Psycho-physics........... A complete description of the relationship existing between visual cerebrosis and visual sensation is given in the expression: 

\[ S = f(C) \]; no relationship between two physical processes can be wholly described by an equation. Physical events are correlated, but they are also connected with each other by bonds of energy or matter or both. We describe this relationship which exists between the physical series and the psychical consequents or concomitants as that of psycho-physical parallelism. This parallelism is purely formal and consists in the causal dependency expressed in the above functional formula, and in nothing else. The assumption that all psychical events can be completely represented as functions of definite physical events we shall speak of as the fundamental assumption of psycho-physics; it is a postulate without which we cannot argue.

A Further Assumption With Regard to the Psycho-physical Relationship....... From a purely scientific standpoint the relationship expressed in the principle of psycho-

physical parallelism remains without explanation. Physical hypo-
thesis explains—or tends to explain—all of the other cor-
relations existing among phenomena, as they are observed by the scientific mind, but physical hypothesis has never even pretend
ed to explain this one. Now from the view-point of our thesis the meaning of the psycho-physical relation is very important, for almost all of the data which we shall be obliged to employ are psycho-physical in character; they are formulations of ob-
erved correlations between neural and sensory structures and changes. Now although from a purely scientific point of view no rationale of the psycho-physical relation is possible, this is far from being the case if we rise to the higher view-point of epistemology. From this place of vantage we see that the physi-
cal series of events which constitutes the first section of the causal chain which as a whole is visual response, is a fabrica-
tion, its component parts being merely symbolic representations --in terms of the common factors of perception--of those reali-
ties of the universe of which the last link in the causal chain happens to be an actual example. We have already considered the foundation of this view in discussing the philosophical mean-
ing of physical hypothesis (cf. page 51). We need not repeat that discussion here. Suffice it to state that, while from a physical or naturalistic standpoint we have no means of deter-
mining the nature of the functional relation which connects C and S--without having actually observed both C and S in process --, we can, with the broader view of epistemology, assert that in all probability it will be of the simplest sort, namely, pro-
portionality, so that if we measure C and S in the proper units, we may write: c = s. It is, of course, a fact that the episte-
mological reasoning which leads to this result is assumptive in
its character and is capable of being upset by actual psycho-
physical experimentation in which both C and S are simultaneous-
ly observed and measured. Since this has not as yet been accom-
plished, it seems advisable to accept the results of a reasonable 
epistemological argument and to discuss the general psycho-physics 
of visual sensation upon the assumption that brain states and 
their psychical correlates are simply proportional.

Two Psycho-physical 
Definitions........

Since the causal nexus which exists 
between physical and psychical events is 
so different from that existing between physical or psychical 
events in continuous homogeneous series, it seems advisable to 
employ a special terminology to designate the relationship in ques-
tion. We shall say that a specific stimulus or physiological 
change consequent upon stimulation, induces the corresponding sen-
sation. This suggests dependency without apparent continuity be-
tween the sensation and the physical processes. A physical struc-
ture necessary for sensation may be said to mediate the sensation 
in its functioning. We shall also, of course, make use of the 
usual term parallel to indicate the entire mode of dependency of 
C and S, but not of S and any other member of the physical series 
of events, any of which, however, may be said to induce the sensa-
tion.

In addition to the above definitions we 
may add two others possessing psycho-physical significance. In 
the discussion of the correlation which exists between sensory 
hue and the wave-length of the stimulating light, we shall find 
it convenient to speak in terms of the spectrum. When we employ 
the term physical spectrum we shall denote the gamut of electro-
magnetic waves only; by the visible spectrum we shall mean the 
series of sensations induced by these waves.
Section XIII: The Psychological Experiment and the Question of the Veridicality of Introspective Reports.

Description of the Psychological Experiment..............

There is a certain formal conception the use of which will aid us in the discussion of visual response.

This is the conception of the psychological experiment. The typical psychological experiment is carried out by two individuals, one of whom engineers the experiment while the other makes introspective observations and renders an introspective report. Now from the standpoint of either psychology or metaphysics the experimenter and the observer—as these two individuals are denominated—are simply consciousnesses; they are minds, or unit intelligences. As such we shall symbolize them by E and O respectively. By E we designate the total experience or subjective of the experimenter, by O that of the observer. So far as the experimenter is concerned, E = himself, and similarly with the observer. We may regard E as an ideally typical human consciousness, but one the volitional department of which is controlled by dominantly scientific interests, and the thought department of which is characterized by rigid logicality in the analysis of scientific results. We may regard O as any sort of human consciousness except that the nature of its perceptions are such that they lead to perfectly accurate description of those subjective processes of O which are being observed in any psychological experiment. The typical experiment consists in the arrangement of the conditions of the experiment by E (in E and O), a series of observations under these conditions by O (in O), the description of these ob-
servations by $O$ (in $O$ and $E$), and the analysis of these descriptions with reference to the experimental conditions—and their meaning—by $E$ (in $E$). This we shall speak of as the psychological experiment (par excellence), and whenever the letters $E$ and $O$ are employed in our discussion they will imply the above described situation, unless otherwise specified. From the standpoint of $E$, $E$ is wholly subjective, and $O$ wholly objective. The physical phenomena which constitute the so-called conditions of any experiment are merely certain departments of $E$ and $O$, but more especially of $E$. With reference to other possible interpretations of these phenomena we have already had something to say in discussing the meaning of hypothesis.

There are certain corollaries of the situation presented in the psychological experiment which are of fundamental importance to the investigator of visual response. This investigation depends in large measure upon the acceptance of introspective reports of observers whose organisms are subjected to experimentation. In such examinations as those of so-called color-mixture the experimenter may regard the situation from a purely physical standpoint, the report of the similarity of the induced sensations (cf. page 70) which is given by the subject being viewed simply as a physical test of similarity of physical response. A report of difference may be regarded in the same way. But when the nature of the report is such as to yield specific rather than relative information more care is necessary in its interpretation. For example, when the observer asserts that two sensations are the same, there can be no doubt in the ex-
perimenter's mind (i.e., in E) that the parallel cortical processes are the same. But when a particular observer also adds that they both possess the attribute of greenness, the experimenter cannot be certain—in the first instance, at least—that the parallel cerebrosis is the same as that which is connected with the report greenness from another observer. Locked at metaphysically, he cannot be positive that the sensation which is described really is green. Whether or not meanings and words correspond as we pass from one observer to another must depend upon the similarity or difference of the psychological histories of the observers in question. Let us examine this problem more in detail.

The Primitive Foundation of Verbal Intercourse. The primary value of language as a method of communication between men lies not in its indication of the subjective states of the individuals concerned but in the indication of specific real stimuli or objective conditions common to both. This is so true that the identity of meanings in different consciousnesses can be regarded in the last analysis as an identity of objective (partly as physical) meaning rather than an identity of the subjective states which each individual actually connects with the words which he employs. Suppose that two individuals decide to use the symbol A' for a specific meaning which they desire to mutually consider in discussion. In what way will they attempt to make sure that each means the same, when this symbol is employed. Let us assume that one of the individuals, E, already connects the symbol A' with a particular perception, sensation, or other content of his own consciousness which we may re-
present by \( \mathfrak{f} \). Within \( E \) the meaning of \( A' \) is \( \mathfrak{f} \). Now he desires to discuss \( \mathfrak{f} \) with another individual, \( O \), and in order to do this it is necessary that he should "convey" his meaning, \( \mathfrak{f} \), to \( O \). Since \( \mathfrak{f} \) is not itself a symbol but is, instead, some averbal element in \( E \) (or possible \( E \)), \( E \) will be forced to "convey" his meaning to \( O \) by a process of exemplification; he will be obliged to "show" \( \mathfrak{f} \) to \( O \). But this is not an easy matter, for \( \mathfrak{f} \) as a content of \( E \) cannot become in reality also a content of \( O \). What \( E \) will actually do will be to subject both \( O \)'s organism and his own to the same stimulus, \( P' \). He will then assure \( O \) that what he means by \( A' \) is the particular modification of consciousness which both \( O \) and \( E \) experience on account of this particular stimulus. One \( E \)'s part this is \( \mathfrak{f} \), on \( O \)'s we may represent the conscious modification by \( \mathfrak{f}' \). Now in the last analysis this method is the only one which can be employed in the fixing of meanings between men. It can easily be seen that while it is perfectly satisfactory with reference to the stimulus--\( A' \) in both consciousesses, \( E \) and \( O \), being connected with the same stimulus, \( P' \)--it may be quite unsatisfactory with respect to \( \mathfrak{f} \) and \( \mathfrak{f}' \). These may or may not be similar, according to the similarity or non-similarity of the response of the two organisms to like stimuli, that is, according to the likeness or difference of the organisms in relationship with the stimulus. In common life meanings are satisfactorily fixed if the same word, spoken by different men, indicates a common stimulus, a common environmental condition, but in psychology this is, of course, not the case; here the only significant meanings are the subjective states, \( \mathfrak{f} \) and \( \mathfrak{f}' \). In every-day experience these meanings are identified by
each individual, with the object; no clear distinction is made between stimulus and stimulus effect, but in psycho-physical investigation we are forced to discriminate sharply between these two factors, and we recognize that the common-sense identification of $\Psi$ with $\Psi'$ with $P'$ is entirely fallacious.

The Primitive Situation in Psychological Meaning

Now when in an experiment upon visual response an observer reports that the sensation, $S'$, induced by a particular light, $L'$, is describable by the word green ($= G$), what interpretation is it legitimate that the experimenter should give to this report. Obviously, without making any gratuitous assumptions (such as that underlying metaphysical argument), he can only say that $S'$ has a quality similar to that which $O$ has always been accustomed to associate with $G$ (the symbol); he cannot, in the first instance, assert that the quality is the same as that with which he, $E$, connects the symbol $G$. What he may assert, however, is that stimuli which induce greenness in his own visual field induce the same or some other quality, $\Psi'$, in $O$'s field, and that, with the same stimulus, $L'$, in each case, the relationship between $G$ and $\Psi'$ is constant.

The Reality of the Present Problem...

Now the problem of the actual similarity or dissimilarity of $G$ and $\Psi'$ is one which may be put in all good faith. Some investigators have regarded this problem as an illusory one; they have asserted that, it is, somehow, either illegitimate or intangible. This is not the case. $O$'s psychosis is as real and as concrete an existence as anything in the universe; it is indefinitely more real than any characteristic of the physical world. As such a reality it
possesses certain special attributes which, when adequately described, can yield only a single formula. This is equally true of E's psychosis. If O's visual sensations exist, they exist as green, or red, or blue, or as combinations of these, or as some other unformulated quality; they are absolute and in no way relative existences, for a relative existence is always a fiction. If we are not afraid of the metaphysical point of view we need not deny these realities.

But the problem of the similarity of G and \( \Psi' \) is most significant in connection with our present physiological discussion on account of the implications of the sensation quality with the nature of the parallel cerebrosis. If \( G \) and \( \Psi' \) are not the same, then the parallel cortical conditions, \( C_G \) and \( C_{\Psi'} \), cannot be the same, and, hence, the underlying visual mechanisms must be different. When these differences are radical the visual responses involved must belong to different species (cf. page 411). But this argument may be given in the converse form, so that we are led to conclude that when biometric results place any variant under a specific type the parallel sensations are approximately those characterizing the type in so far as the latter is regarded as possessing a psychical aspect. We may, then, conclude that E is only justified in believing that \( \Psi' \) and G (in the case in point) are alike when he has evidence that the observer and himself, O and E, belong to the same species, are representatives of the same type of visual response. This conclusion will have an important bearing upon our argument, for a great deal of the current discussion
of so-called color-blindness is implicitly based upon the assumption that the introspective reports of the dyschromatic subjects can be accepted upon their face value. We are right in assuming that the sensations experienced by other individuals under specific conditions of stimulation are very closely similar to those which we ourselves experience when placed under the same stimuli if we have physical (biometric) evidence that these other individuals belong to the same germinal species (cf. page 41) as ourselves, when they are studied with reference to visual response. We are apt to be in error, if we make this assumption when there is evidence to the contrary.

Symbolism of the Above Discussed Situation............. In the subsequent use of the ideas brought out in this discussion we shall employ the symbolism of the psychological experiment, E being the consciousness of the experimenter, and O that of the observer. We shall employ the symbol A' as a general sign for any word used in common by E and O in the designation of specific visual attributes or changes. We shall suppose E to represent the ideal normal type of visual response and the meaning of A' in E is \( \Psi \), while its meaning in O is \( \Psi' \), the common stimulus being P'. Then we have the rule: If O belongs to the normal species, \( \Psi = \Psi' \) (approx.), but if O does not belong to the normal species, but belongs to some anormal species (cf. page 41) either \( \Psi = \Psi' \) or \( \Psi \neq \Psi' \), according to the nature of the anormality. In the latter case, if the anormal type in question should prove to be merely a reduction of the normal, it should be possible to determine what sensation quality in E, the meaning \( \Psi' \) does, in point of existence, resemble.
PART FIVE: A REVIEW OF CURRENT HYPOTHESES CONCERNING THE NEURAL MECHANISM UNDERLYING VISUAL SENSATION.

Section XIV: Mechanical Hypotheses of Visual Sensitivity.

Mechanical Aspects of Young's Theory........ The extant hypotheses concerning the mechanism underlying visual sensation may be divided into three classes, the mechanical hypotheses, the chemical hypotheses, and the electrical hypotheses.

The mechanical hypotheses naturally possess the most ancient lineage. Newton in his Opticks1 suggested that color perception might be explained by assuming that the impact of the corpuscles which he supposed to constitute light set up—in the retina and the connected nerves—vibrations of different intensities and kinds, according as the exciting corpuscles were larger or smaller, corresponding with rays of differing refrangibility. The hypothesis of Thomas Young as it was originally proposed was undoubtedly mechanical in its meaning, but it was less crude than the interpretations which have been made of it by others. Young assumed that every point in the retina of the eye was supplied with three sorts of labile particles which were capable of vibrating in synchronism with three different frequencies of light; he did not assert the existence of vibrating "fibres", but instead—being a thinker much in advance of his time—he anticipated very clearly the modern molecular hypothesis. In the hands of Helmholtz Young's theory became largely a convenient means of formulating the phenomena of color vision rather than a defin-

1 NEWTON, ISAAC: Opticks; (1706); Qu. 16, 13, 14.
ite hypothesis, but although Helmholtz continued for a long
time to speak of the "red, green, and violet fibres" the general
tendency of later day advocates of the hypothesis has been to
interpret the three fundamental sensibilities in chemical terms.

Charpentier's Hypothesis...

Charpentier has interpreted visual response mechanically, even supposing that color
is the more or less accidental result of interference effects occurring between two different sorts of neural oscillation.
His hypothesis makes some use, also, of electrical reactions.
Its unimportance and complexity make it inadvisable to exposit it here in detail.

Theories of Selective Vibrations in the Retinal Cones.

Charpentier postulates the existence in the retinal-cerebral apparatus of two
distinct mechanisms of visual response, the photesthetic and the visual; one of these, the first, corresponds with the retinal rods and their connections; the other is made up of the retinal cone system; sensations of color result from the superposition of vibrations produced in both of these systems simultaneously. In this country G. Stanley Hall was one of the first to suggest that on account of the tapering of the external segments of the retinal cone cells, different parts of these segments were structurally adapted to respond mechanically to different rates of vibration. This idea has been inde-

Patten's Hypothesis....

Patten of Dartmouth College independently elaborated by Professor William

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1 CHARPENTIER, A: La Lumiere et Les Couleurs; (1888); p. 265.
2 HALL, G. S.: in Amer. Acad. of Sci. and Arts; (1878), vol. 13, p. 402.
3 PATTEN, W.: A Basis for a New Theory of Color-Vision; American
Naturalist; (1899); vol. 32, no. 383, pp. 832-857.
tive cells in the eyes of certain invertebrates exhibit fine fibrils placed at right angles to the line of motion of the light rays, and noting the fact that in many cases the cells in question are conical or pyramidal in form, and so present transverse fibrils of varying length, he arrives at the conclusion that the cones of the human retina are delicate resonators tuned to respond to the various frequencies of light. One gathers from the trend of the argument in the first part of the paper that a mechanical vibration of these "retinodial fibres" is imagined to occur; finally, however, the author compares the radial formations which sometimes exist to batteries of Hertz resonators, and pointing out the presence of similar arrangements in the "punct substance" of the brain of the invertebrates near the optic ganglion, he supposes that the oscillations set up in these resonators by the light is reproduced in the brain as the immediate parallel of the sensation.

A somewhat similar theory is that of Antoine Pizon, who has noticed certain vibratory movements of the pigment granules of the visual cells of vertebrate and invertebrate animals, and supposes that in the case of the eyes of the higher vertebrates the pigment grains of the retinal epithelium are the actual elements sensitive to the light. These are imagined to be of various sizes, and by responding to light vibrations of various frequencies, they are supposed to set up similarly specialized vibrations in the rod and cone cells with which they are in immediate contact.

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1 PIZON, A.: Théorie mécanique de la vision; Compt. rend. Acad. d. Sci.; (1901); tome 133, pp. 835-837.
Bernard, who has advanced the idea that the movement of the retinal epithelium is the fundamental change underlying visual sensation, and supposes that the nerve currents taking origin in the rod and cone cells are determined by different degrees of pressure exerted upon these cells by the epithelial elements.

Another mechanical hypothesis, which makes use of chemical conceptions as an auxiliary, is that of Dr. Adolph Stöhr. This writer assumes the existence in the retina of two light sensitive mechanisms: the visual corpuscles, which consist of fibrils bearing on their surfaces flat plates in sets of four, each member of the set being made of a special material; and, in addition, certain visual substances. Under the action of heterogeneous light the plates of the visual corpuscles all vibrate in a similar manner, inducing the sensation attribute of white. Homogeneous lights, however, bring about the production of special visual substances which also exhibit vibrations, with the result that the oscillations of the plates are modified in accordance with the reactions occurring between the special material of the plates and the visual substances.

1 BERNARD, H. M.: The Sense of Sight: A Sketch of a New Theory; Annals and Mag. of Nat. Hist.; (1898); vol. 17, .
2 STÖHR, ADOLPH: Zur Hypothese der Sehstoffe und Grundfarben; Leipzig & Wien; Deuticke; (1898); 103 pages. See Ladd-Franklin (C.L) in Psych. Rev. (1900); vol. 7, p. 415.
Section XV: Chemical Hypotheses of Visual Sensitivity.

The Young-Helmholtz Hypothesis..............

The Young-Helmholtz hypothesis in its modern form is, so far as it is hypothetical rather than a mere shorthand expression of the facts of color mixture, a typical representative of those hypotheses which make the mechanism of visual response fundamentally chemical in nature. According to the modern interpreters of this hypothesis there exist in the retina, presumably in each cone cell, three distinct substances which respond to the presence of light of various wave-lengths by a measured rate of decomposition. If these three substances are denoted by the symbols $M_r$, $M_g$ and $M_b$, and their concentrations in the retinal element affected are $m_r$, $m_g$ and $m_b$, the respective rates of decomposition can be represented as $\dot{m}_r$, $\dot{m}_g$, and $\dot{m}_b$. (cf. page 61)

The rate of decomposition of each substance is dependent upon two factors, the energy and the wave-length of the light falling upon the retinal element considered (cf. pages 233 ff). Supposing the energy to be constant, we can write: $\dot{m}_r = f_r(\lambda)$, $\dot{m}_g = f_g(\lambda)$, and $\dot{m}_b = f_b(\lambda)$. According to the Young-Helmholtz hypothesis these three functions have maxima with wave-lengths of approximately 750, 505, and 470 respectively, corresponding in the visible spectrum with red, green and blue. The Young-Helmholtz hypothesis is rooted in the doctrine of specific nerve energies, and for that reason it is safe to assert that the most generally accepted view with regard to the further consequences of the retinal response above described is that each

decomposition excites a specific neuro-fibril (cf. page 229) so that the central neurones go through a process possessing three separate aspects corresponding with the three retinal decompositions and quantitatively dependent upon the latter. According to König, who has been foremost in the development of the three component hypothesis the visual yellow which results in the partial bleaching of the purple pigment of the rods, is to be identified with the substance $M_b$, having a maximum rate of decomposition with $\lambda = 470$, while the substances $M_r$ and $M_g$ are to be located in the pigment epithelium.

Hering's Theory. The psycho-physical problem of the mode of correlation of the three fundamental processes postulated in the Young-Helmholtz hypothesis, with the attributes of the elementary visual sensation has received very little attention at the hands of advocates of that hypothesis. For this reason the hypothesis merits small consideration as an attempt to offer any but a partial and proximate solution of the problem of the visual mechanism. The theory of Ewald Hering upon the other hand (cf. page 96) is founded upon a psycho-physical analysis, and it is perhaps more typically a chemical hypothesis of the visual mechanism than that of Young and Helmholtz. An attributive analysis of the elementary visual sensation yields six distinct and fundamental variables which we have denoted by the symbols: $r, g, b, y, b, \text{ and } w$. In our analysis (cf. page 96) we have noted the mathematical antagonism which exists between $r$ and $g$ and $y$ and $b$, as well as the reciprocal relationship of 1 König, A: (Title not found); Sitzungsbd. der k. Akad. d. Wissenschaften; Berlin; (1894), S. 577.
b and w. Now Hering—like Young—postulates the existence in the "retino-cerebral apparatus" of three distinct substances. These substances we may symbolize by $M_{yb}$, $M_{rg}$, and $M_{bw}$, and the corresponding concentrations by $m_{yb}$, $m_{rg}$, and $m_{bw}$. These three substances may be located either in the brain or in the retina, or possibly in both places. As in the modern Young-Helmholtz theory the sensitive substances are supposed to change in concentration under the action of light of various wave-lengths. Change in concentration may be of the order either of increase or decrease, so that we may describe six possible processes in the fundamental substances as follows: (1) $\dot{m}_{rg}$, (2) $-\dot{m}_{rg}$, (3) $\dot{m}_{yb}$, (4) $-\dot{m}_{yb}$, (5) $\dot{m}_{bw}$, and (6) $-\dot{m}_{bw}$. The rate of each of these processes—as in the Young-Helmholtz hypothesis—is representable as a function of the wave-length of the stimulating light and of the energy of the light, so that: $\dot{m}_{rg} = f_{rg}(\lambda, e)$, $\dot{m}_{yb} = f_{yb}(\lambda, e)$, and $\dot{m}_{bw} = f_{bw}(\lambda, e)$, it being possible to combine the positive and negative changes in a single function.

The function $f_{rg}$ is of such a character as to possess a minimum at $\lambda = 750$ (approx.), a value of zero at $\lambda = 574.5$, a maximum at $\lambda = 495$, and a second value of zero at $\lambda = 471$. The function $f_{yb}$ exhibits a minimum at $\lambda = 574.5$, is zero at $\lambda = 495$, comes to a maximum at $\lambda = 471$, and is again zero at $\lambda = 400$. The function $f_{bw}$ is zero at $\lambda = 800$ and $\lambda = 400$, and sinks to a minimum at about $\lambda = 500$.

It is obvious that the psychophysical relationships of Hering's hypothesis are described by the formulae: $r = f(-\dot{m}_{rg})$, $g = f(+\dot{m}_{rg})$, $y = f(-\dot{m}_{yb})$, $b = f(+\dot{m}_{yb})$ and $w = f(-\dot{m}_{bw})$. Hering adds a further supposition. When there is an absence of stimulation ($e = 0$) in one region of
the retina with concomitant presence of stimulation in another
the function $f_{bw}$ may have a positive value, so that $b = f( + \hat{m}_{bw})$.
This makes it apparent that there are important variables in
these functions other than the wave-length and energy of the
stimulating light. These variables are defined in Hering's theory of metabolism, which we shall later consider more at length.

Amplifications of \textit{Hering's Hypothesis}. Hering himself makes no definite
assumptions with regard to the retinal basis of the processes above described. Ebbinghaus and G. E. Müller have brought forward certain proposals in this regard.
According to Müller the assumption of a cerebral black-white sub-
stance—the remaining two substances being considered to be reti-
nal—removes certain difficulties which must otherwise be
faced by Hering's hypothesis, in particular the difficulty that
there is no yellowish-blue and greenish-red sensation correspond-
ing with the blackish-white which we call gray. Ebbinghaus sup-
poses that the yellow-blue substance of Hering's hypothesis is
identical with the visual purple, which in its initial form is
yellow-sensitive, and in its transition—visual yellow—stage
is acted upon by lights inducing the sensation attribute of
blue. This pigment also occurs in the cones, to-gether with
the red-green substance, the effect of the presence of the two
being a mutual masking of objective or physical color, so that
the substance of the cones appears colorless. The black-white
substance is also said to exist throughout the retina.

1 The facts concerning Hering's theory come mostly from W.H.R.R. pp. 1112-1121.
2 EBBINGHAUS, H.: Theorie des Farbensehens; Zeits. f. Psych. u.
Physiol. d. Sinne; (1893); Bd. 5, S. 145-238. Cf.
3 MÜLLER, G. E.: Zur Psychophysik der Gesichtserscheinungen;
Zeits. f. Psych.; (1896-7), Bde. 10, 14.
The Hypothesis of Donders...

The chemical hypothesis of F. C. Donders is more specific in character than either the Hering or the Young-Helmholtz hypotheses. Donders enters into details with regard to the chemical mechanism, and assumes that in the neurons mediating the sensation there exist certain molecules made up of eight radicles. These molecules are capable of being decomposed under the influence of the nerve impulses received from the retina. Complete decomposition into eight elements is regarded as the physical parallel of the sensation attribute of whiteness, \( w \); partial decomposition furnishes a basis for the hues. If we imagine the eight radicles making up the molecule to be arranged at equal distances upon the circumference of a circle, cleavage along a certain diameter would yield the cerebral parallel of B; subsequent symmetrical cleavage of the two halves would furnish the parallel of Y. Initial cleavage along a different diameter, as shown in the accompanying figure (Fig. 2.) would, however, result in the sensory attribute R, while a second splitting at right angles would give G. The retinal substances are supposed by Donders to be three in number, responding after the manner of the original fundamentals of Young's hypothesis to lights forming the stimulus to sensations having the qualities R, G, and violet, respectively. From the standpoint of stimulus the mathematical representation of these excitabilities is the same as in the Young-Helmholtz hypothesis; from the standpoint of sensation quality, it is the same as in Hering's theory. Donders postulated no rigid linking of elementary cerebral and retinal excitations. The relation existing between Donders' retinal triad and his cerebral tetrad is

1 DONDERS, F. C.: in Arch. f. Ophth.; (1881); Bd. 27, Abth. 1, S. 55; also ibid. (1884); Bd. 30, Abth. 1, S. 15.
Fig. 2.

DIAGRAMMATIC REPRESENTATION OF THE CEREBRAL MOLECULE OF DON- 
DERS' HYPOTHESIS.

The four possible symmetrical modes of cleavage correspond 
with the four simple hues as described in the text.
the same as that existing between the three substances of the
Young-Helmholtz theory and the hues. The sensory attribute of
blackness (shade) was accredited by Donders to a condition of
minimum—but not complete absence of—activity in the cortex.

Mrs. Ladd-Franklin's Hypothesis another chemical hypothesis of
great merit is that proposed by Mrs.

Christine Ladd-Franklin. Mrs. Ladd-Franklin postulates the existence in the cone-cells of the central retinal region of a substance the molecules of which are made up of a nucleus and three side-chains. One of these side-chains is double. The nucleus is held to be chemically stable, while the side chains may be easily broken away from it by external forces. The natural period of vibration of the simpler side-chain corresponds with that of light of wave-length 470, and so it resonates when acted upon by light-waves of this dimension, thus absorbing energy and becoming detached from the nucleus. When thus detached it becomes the specific cause of the sensation attribute B. The components of the other side-chain resonate with lights of wave-lengths 750 and 505 respectively, and form the specific bases of the sensation attributes R and G. The entire side-chain, however, is broken off when equal stimulation of its two components occurs and so forms the physiological substrate of the attribute Y. Simultaneous disruption of both side-chains offers a foundation for W. An evolutionary explanation of the meaning of this molecular mechanism is given, it being assumed that the molecule has been differentiated from an original vaguely selective system—which gave the W reaction for all lights—through a form giving the

1 LADD-FRANKLIN, C.: Eine neue Theorie der Lichtempfindungen; (over)
2 Mrs. Ladd-Franklin gives no figures, but since she bases her argument with reference to the limitations of physiological response upon König's determination of the "fundamental sensations" it seems advisable to make the statement of the hypothesis physically definite by the use of König's figures.
attributes Y and B, to a final modification as above described. The primitive stage of the molecule is supposed even now to exist in the sensitive substance of the rods, while the second stage is represented in the outer "red-green blind" regions of the retina. This hypothesis has been elaborated by Schenck.

Wundt's Hypothesis... Wundt, who reacts from the view that the quality of visual sensation can be regarded as constituted by a combination of definite attributes, and therefore postulates the existence of only two visual substances, one the decompositions of which underlie the attributes of tint, while the hues are accounted for in the manifold and graded mutations of a single other substance.

The Postulates of Von Kries...... The untiring labors of Professor Johannes von Kries of the University of Freiburg im Breisgau have been mainly directed towards the support of the hypothesis that the rods of the retina are principally concerned in vision under conditions of low illumination and are achromatic in function, while the cones act as color-perceiving organs. Von Kries specifies two distinct physiological causes of W, first and fundamentally, the excitation of the rods, and secondly a "psychically reconstructed" W based upon equal stimulation of all of the specific light sensitive substances of the cones. (vide page 334)

The Hypothesis of Edridge-Green.... Von Kries' theory of the retino-cerebral process is merely a modification of the Young-Helmholtz theory by the addition of a special W induc-

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1 SCHENCK: Arch. f. d. ges. Physiol.; (1907); Bd. 118, S 129.
2 WUNDT, W.: Physiologische Psychologie; (1893); Bd. 1, S. 535.
ing, or energy sensitive substance, the visual purple. In addition, however, to Ebbinghaus' attempt to utilize this well known retinal pigment in a realistic presentation of Hering's hypothesis, there are some further speculations concerning its function which are worth mentioning. F. W. Edridge-Green makes the visual purple the basis of a theory somewhat resembling that of Wundt in its general character. He assumes that the sole function of the rods of the bacillary layer of the retina is the secretion of this pigment. The liberation of the visual purple from the rods is dependent upon the action of light, and a number (five or six) of different varieties of the pigment are supposed to exist, and these are liberated by light of special wave-lengths. The light sensitive substances thus set free stimulate the cones, a qualitatively as well as quantitatively differentiate impulse being sent to the brain. In the brain, separate light and color perceiving neurons are supposed to exist; the impulse first passes to the light ($C_{bw}$) sensitive center and there induces a sensation attribute of $W$; it then goes to the "color perceiving" centers which vary in number—or, at least, in differential sensibility—according to the power of the individual to discriminate between lights of various wave-lengths. 

Oppolzer's Theory.... Another chemical hypothesis—and one possessing slight merit—is that of von Oppolzer who—

with König—believes that the seat of the changes set up by the impact of light upon the retina is the pigment epithelium. The changes there initiated stimulate the rods and cones. If only a single cone is acted upon the induced sensation is charac-

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1 EDRIDGE-GREEN, F. W.: The Hunterian Lectures; Lond. (1911).
terized by the attribute W; the hues are due to the simultaneous
stimulation of several adjacent elements. Color thus becomes,
as in the theories of Charpentier and Goller (to be mentioned
later) a species of interference phenomenon, the sensation of
white, only being fundamental.

Preyer's Theory: The visual hypothesis of W. Preyer, is expres-
ed in terms which are physiological rather than
chemical, but it may fairly be considered as chemical in its
ultimate meaning, although—as we shall note at a later point—it
contains some electrical factors. According to Preyer each
fibre in the optic nerve which is capable of mediating all of
the attributes of the elementary visual sensation ends in the
retina in two cones. One of these cones, it is asserted, is stimu-
lated by lights of relatively long wave-length while the other
is excited by lights of relatively short wave-length. Impulses
set up in the latter, if they reach the brain, are paralleled
by the "cold" hues, G and B, while those originating in the for-
mer type of cones induce the "warm" hues, R and Y. As in Charpen-
tier's hypothesis, however, these separate impulses are capable
of interfering with each other. This interference is stated to
occur in the large "ganglion cells" of the inner retinal layers.
The conflicting impulses result in the production of a new type
of impulse which is paralleled at the brain by the sensation
attribute of W. The impulse itself is figured as "vibratory."

Section XVI: Electrical Hypotheses of Visual Sensitivity.

Edridge-Green imagines the mode of stimulation of the cone cells by the visual purple (cf. page 135) to be electrical in nature. There are several other hypotheses which make the fundamental mechanism of vision depend upon electrical states or changes. Perhaps the first of these to be advanced was that of Preyer, the general nature of whose theory we have already indicated. Preyer bases a conception of the process of stimulation of the optic nerve endings upon Du Bois-Reymond's law that only a changing electrical condition can result in nerve excitation. The action of light is supposed to bring about an electrical variation in the retina with consequent stimulation of the nerve. Restoration of electrical equilibrium means adaptation and the disappearance of the characteristic sensation quality.

Peddie, Stokes and Nicati... Dr. William Peddie has proposed a photo-electrical hypothesis which is apparently of an analogous nature; the writer has not been able to find a copy of his original paper. Sir G. G. Stokes observes that the laminated structure of the rod and cone endings resembles that of an electrical battery, and suggests that these retinal cells are galvanized by the photochemical changes occurring in the visual purple, the result being a visual impulse. He cites the experiments of Dewar and M'Kendrick upon the electrical variations occurring...

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1 See PREYER, W.: Die Empfindung als Funktion der Reizänderung; Zeits. f. Psych. u. Physiol. d. Sinn.; (1894); Bd. 7, S. 241.
3 STOKES, G. G.: The Perception of Light; (1895); Nature, pp. 66-68.
ring in the frog’s eye under the influence of light, and also makes use of the analogy of the electrical organs of fishes, which possess a structure similar to that of the rod and cone cells. Another electro-chemical hypothesis is that of William Nicati, who places the light-sensitive substances in the pigment epithelium, and supposes that the elements of the bacillary layer of the retina are stimulated by electrical changes resulting from the photochemical process.

Two Hypotheses Based Upon Optical Conceptions.............

In connection with the above mentioned hypotheses involving assumptions with regard to the electro-physiological effects of light upon the eye, we may note the existence of certain hypotheses founded upon purely optical principles. One of these is the hypothesis of Goller. This thinker supposes that the thin transparent plate which separates the external from the internal elements of the rod and cone cells brings about a circular polarization of the light passing through it. The degree of polarization is a function of the wave-length of the light, and Goller imagines that the hues are dependent upon the degree of circularity of the light oscillations thus polarized, while luminosity is determined by the crude intensity of the rays. No account of the differentiation of the visual impulse to correspond with this sensibility to degrees of circularity in polarization, is given. A second optical hypothesis is that of G. Darzens, who supposes that the light is reflected from the pigment epithelium in such a way as to produce standing waves—the result of the interference of the incident and the reflected ray

1 NICATI, W.: La Psychologie Naturelle; Paris; (1898).
2 GOLLER: Die Analyse der Lichtwellen durch das Auge; (1869); Du Bois-Reymond’s Archiv.
---within the cone and rod segments. The dimensions of these standing waves determine the character of the excitation of the optic nerve fibres and thus enable the hue of the sensation induced to become a function of the wave-length of the stimulating light.

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are "links" in lines of electrical force, which travel along.

PART SIX: THE MECHANISM OF VISUAL STIMULATION.

the force-lines, such as a wave moves along a snail rope, ex-
cept that one is placed not in a lateral movement, but a
change in electrical potential. When a light-wave is passing
through any little region of space it means that electrical for-
tes in that region are changing--oscillating--in a direction at
underlying visual sensation. It is now intended to examine the
right angles to the sense of motion of the wave, and then as
fundamental conditions which must limit all hypotheses of this
sort and then to attempt--from a thoroughly physically realistic
point of view--the critical reconstruction of a maximally proba-
ble hypothesis, out of the materials presented by the facts of
vision and by the speculations which we have just epitomized.

The Electrical Na-
ture of Light..... The first link in the chain of ele-
ments which to-gether must be imagined as constituting the physical division of visual response (cf.
page 60) is customarily light. This is the normal visual stim-
ulus (P = L), and its nature requires a somewhat detailed con-
sideration. It is to be understood that our account of the na-
ture of light--like that of all of the factors which are to be
considered as constituting the principal subject-matter of this
thesis--is an account of an hypothesis. This does not mean, how-
ever, that there is any appreciable uncertainty concerning the
validity of the hypothesis of radiation which is to be describ-
ed.

Light is spoken of popularly as a matter of trains
of waves or undulations in the luminiferous aether. In the
strict physical sense, however, this description of light is er-
roneous; the oscillations which comprise a beam of luminous radi-
ation are not molar, or even molecular, but are electrical and 
magnetic, or, in a single word, are electro-magnetic. Light-waves
are "kinks" in lines of electrical force, which travel along the force-line, much as a wave moves along a shaken rope, except that the displacement is not a material movement, but a change in electrical potential. When a light-wave is passing through any little region of space it means that electrical forces in that region are changing--oscillating--in a direction at right angles to the sense of motion of the wave, and that at right angles to both, magnetic forces are similarly vibrating. Such an electro-magnetic oscillation can only be set up by the rapid backward and forward motions of an electrical charge--in the case of light, of the electrons within the atoms of the luminous body--, and they can act only upon electrical or magnetic systems. The physical stimulus acting at the retina is, then, electro-magnetic, and the retinal response must depend upon the electrical or magnetic properties of the retinal substance.

The Frequency and the Wave-length of Light. The velocity at which a "kink" set up in an electrical force-line moves in space is a constant, no matter what the magnitude of the kink may be. Hence the waves set up by the oscillations of a vibrating electrical charge have a length which is inversely proportional to the frequency at which the charge is oscillating. When the rate of oscillation is comparatively slow, as in the discharge of the Leyden jar, the waves set up may be several meters from crest to crest, but when the rate of oscillation is relatively rapid the wave-length becomes proportionately small, so that when a particle of matter is chemically or electrically excited the oscillations of the electronic charges bound up within or upon the atoms, being very rapid, set up waves as short as and sometimes shorter than a millionth of a millimeter.
However, the important attribute of any element of electro-magnetic radiation is not its wave-length but its frequency. Since all of the literature upon the subject of the relationship of visual sensation with the varieties of light describes the latter in terms of wave-length rather than frequency, we shall employ this index (λ) in our discussion, but it should be kept in mind that this is merely a rather awkward way of expressing the frequency (n), which is equal to the quotient of the wave-length into the velocity of light in free space: \( n = \frac{3 \times 10^{10}}{\lambda} \). As a matter of the exact theory of light, the wave-length of any element of radiation varies in passing through different media, because the velocity varies, but the frequency remains the same. Thus when a ray of light enters the eye, its wave-length is decreased, because it travels more slowly while retaining the same frequency, but this actual change of wave-length is of no importance in the discussion of visual response, if, as seems likely, this response is determined only by frequency. Nevertheless, it can be seen that the use of the wave-length as a means of describing luminous stimuli is inexact and in a very accurate account of the visual process would have to be replaced by the frequency since this alone is constant under all ordinary conditions.

What Determines the Nature of a Light Ray....

Electro-magnetic radiation is not necessarily constituted by trains of symmetrical waves of uniform length. The character of any travelling electro-magnetic disturbance is wholly determined by the nature of the acceleration changes occurring in the electrical charge originating the pulse. The fact that the sort of dis-
turbance which we call light is uniform in constitution is de-
pendent upon the conditions governing the movement of those
particular electrical charges from which the light radiation takes
origin. These charges, as we have stated, are the intra-atomic
electrons, or electron-groups--or, possibly, molecular ions--
which characterize the various elements and compounds of matter.
When excited by chemical or electrical changes these electrons
or electronic systems vibrate in their natural periods about
certain fixed neutral positions and in so doing set up the oscil-
lations in their electrical fields which radiate in the form of
light; the radiation is wave-like in character because the os-
cillations of the intra-atomic charges follow the periodic law;
it is uniform for the same reason. Certain electro-magnetic
radiations--such as the X-rays--are not of the periodic charac-
ter, but are single pulses; these correspond to a sudden release
of an electron from the influence of some confining force, and
there is thus no tendency for oscillation. It is important to
bear in mind this fact, that the geometrical properties of an
element of light are wholly determined by the mode of motion of
the electrical charges which initiate it.

The Intensity of a Light Ray..... In addition to this more or less acci-
dental property of uniform wave-length or
frequency which is exhibited by certain electro-magnetic dis-
turbances, there must be mentioned the attribute of specific in-
tensity. The intensity of light is dependent upon the magnitude
of the radiating charge, and upon the amplitude of its oscilla-
tions. Using the schema of the kinked line of force, we say that
light is more intense the more lines of force there are passing
through a unit surface at right angles to the path of the light, and the more strongly the lines are kinked. Light intensity may be defined in terms of energy. Electro-magnetic radiation is radiant energy; each element of radiation represents a certain portion of the energy lost by the oscillating source, and since radiation elements have a definite volume, we can speak of the energy density of radiation, or the ergs per cubic centimeter.

The energy density of radiation at any point in space is equal to $\frac{1}{2\pi}$ times the sum of the squares of the electrical and magnetic forces acting at that point, and if we call this quantity $\bar{e}$, we may define the intensity of light as $e = \bar{e}C$, the amount of energy which passes through a surface of unit area, perpendicular to the path of the radiation, in one second ($C$ = the velocity of light in free space).

Symbolism of Light

We shall employ the symbol $e$—often with a subscript $\lambda$ to denote the intensity of particular luminous visual stimuli. The symbol $\lambda$ will be employed, as usual, to indicate the wave-length of the light, where it is understood that what is meant is not the actual wave-length in any region but such a value that $\lambda = C/n$, where $C$ is the velocity of light in free space, and $n$ is the frequency of oscillation (cycles per second) of the electrical and magnetic forces at any point through which the radiation is conceived to be passing, especially, in our case, the sensitive points of the retina. The general symbol which we shall employ for light as stimulus to visual sensation is $L$, the three significant attributes of $L$ being (1) the purity, or composition $P$ (discussed below), which, being determined, permits an analysis of the light into compo-
ments, so that we can write: \( L = L_1 + L_2 + \ldots L_n \); (2) the frequency, \( n \), of each component \( (n = C/\lambda_n) \), replaced, on account of common usage, by the wave-length, where \( \lambda \equiv C/n \); and (3) the intensity, \( I \), of each component. In general, we shall symbolize specific homogeneous lights (see below) by the letter \( L \) with a subscript for the wave length, thus: \( L_{\lambda_1} = L_{550} \). The wave-length will be expressed in double microns, \( \mu \mu \), each of which is equal to one ten-millionth of a centimeter, \( 10^{-7} \) cms.

Homogeneous and Heterogeneous Light

The light falling upon any element of the retina at any time will be either homogeneous or heterogeneous. We shall speak of light as homogeneous when it is of a single wave length, or a single frequency, -- as heterogeneous when it is of two or more frequencies. The number of frequencies exhibited by any light is determined by finding the number of components into which its vibrations must be split in order that all of these component oscillations should be periodic in character. By the purity of a light we mean the reciprocal of its heterogeneity. A light of any degree of impurity can always be regarded as the sum of a certain number of pure or homogeneous lights, and so far as we know the effects produced by a heterogeneous light are equivalent to the effects which would be produced by the sum of its supposed homogeneous constituents.

Light: Certain modern results, both theoretical and experimental, indicate that light radiation must ultimately be thought of, not as continuous, but as made up of little elements or "quanta". According to this view, decrease in the intensity of illumination due to the increased distance of

1 Advanced by Planck.
a receiving surface from a source of light, is not to be explained by an actual decrease in the intensity of elements of radiation, but is due simply to a falling off of the number of elements striking the surface. Moreover the nature of these light quanta appears to be such that, for any frequency, the quotient of the frequency into the total energy is a constant: \( \frac{\epsilon}{\hbar} = \frac{\hbar}{(Wirkungselement)} = 6.65 \times 10^{-27} \) seconds. This conception may prove of assistance in considering the action of lights of various intensities and wave-lengths upon the retina.
Section XVII: The Problem of the Localization of the Sensitive Structures in the Retina.

Light Sensitivity of the Retina... The eye is roughly spherical in shape, the dioptic apparatus being situated in the ventral hemisphere, the light-sensitive elements in the dorsal hemisphere (approximately). There can be no doubt that the region of action of light—the region of light stimulation—within the eye is to be found in the retina, either in the nervous layers or the pigment epithelium which serves as their backing, since the shadows of the corpuscles moving through the capillaries of the inner layers of the retina are very readily perceived subjectively when the eye is subjected to strong uniform illumination.

Structure of the Retina... The retina is a complicated nerve plexus similar in general character to the synaptic or "gray" matter of the brain and cord, especially of the cerebral cortex. It is made up of eight distinct layers, which may be described in centrifugal order as follows: (1) a layer of tangentially running nerve fibers; (2) a layer of very large nerve-cell perikarya, the axons of which form a great part of (1); (3) a relatively thick layer of interlacing tangential and radial fibers made up primarily of the dendrites from the perikarya of (2) and axon ramifications from the perikarya of (4), which is a layer of bipolar cells; (5) a thin stratum of anastomosing tangentially disposed axons and dendrites from (4) and (6), which is a layer of perikarya belonging to the cells of elements of the which (7) the layer of rods and cones are a part. Eighth (8) and
outermost is to be found the layer of pigment cells constituting the pigment epithelium. The retina spreads out over the inner surface of the choroid coat of the eye in such a way as to be present over an area considerably larger than that of the dorsal hemisphere of the organ. Slightly temporal with respect to the optic axis of the eye is to be found the so-called yellow spot or macula lutea, placed somewhat eccentrically within which is the fovea centralis, which forms a depression in the otherwise uniformly smooth retinal surface (with the exception of the point of entry of the optic nerve fibres). The thinness of the retina at this point is due to the absence of all of the neural strata with the exception of that of the cone cells (with their perikarya).

The Five Internal Layers of the Retina are not essential to stimulation Since the elementary visual sensation is at its best in the center of the visual field (the fixation point), and since the facts indicate that the stimulation of the fovea by light induces sensations at the fixation point of the field, and since in the fovea the only elements of the retina present are the cone-cells and the pigment epithelium, it follows that these elements alone are essential in the direct action of light upon the visual mechanism. That the same layer, also, contains the light sensitive mechanisms in other regions of the retina is proven by observations made upon the shadows of the retinal blood-vessels. If the shadow of the same vessel be observed by the use of two sources of light separated by a wide angle, the position of the shadow will be seen to alter. If we measure this displacement of the shadow, know-

1 W.H.R.R. pp. 1099-1100
ing the angle subtended by the two light sources, we are able by a simple application of the geometry of similar triangles to calculate the distance which separates the vessel from the light sensitive surface. The results of such a determination make it appear that this surface is that of the rods and cones. This conclusion should have been anticipated, since the rods and cones are the most distinctive and highly differentiated structures in the retina. The remaining elements of the retinal plexus are such as may appear in any region of neural synapses. If we conceive the retina to have developed from a general into a special form by adaptation of its structure and function to the exigencies of visual response, we should expect the special structures making possible this response to depart most radically from the generalized nerve element. This evolutionary criterion at once indicates the elements of the bacillary layer (7) (cf. page 154) as the light sensitive bodies. The sensitivity of the fovea rules out the five internal layers of the retina: the relative simplicity of the internal (nuclear) half of the rod and cone cells makes it improbable that they possess any specific light responding power, while the high state of differentiation of the external segments becomes inexplicable apart from development in connection with a special visual function. It is possible, however, that the entire rod or cone cell is active in the response, and also that the underlying--or outer-lying--cells of the pigment epithelium are concerned.

Let us examine more closely the morphological properties of these elements.

The Rod and Cone Cells.

Schwalbe has divided the retina into two
regions. The first includes the five inner layers and is called by him the cerebral layer, because it is typically nervous in character, as we have noted above, and structurally resembles the gray matter of the brain. The second embraces the three outer layers, and is denominated the neuro-epithelium of the retina, for the reason that it presents characters diverging from those of purely nervous tissue. From the cytological point of view this region of the retina may be regarded as made up of three different elements; these are the rod cells, the cone cells and the cells of the pigmented epithelium. The rod and cone cells are elongated, radially directed, elements, and are both built upon the same general plan, for each can be divided into three fairly distinct segments, which may be designated as the terminal (outer), the basal (middle), and the nuclear (inner) segments respectively. The terminal portions constitute the outermost reaches of the optic nerve plexus within the eye, and they abut upon the pigment cells, mentioned above. In both the rod and the cone cells these outer portions are made of a substance which is doubly refracting to light, are covered with a delicate membrane of neuro-keratin—which is heavier over the cones than over the rods—which sometimes interferes with the tendency which both elements show to split up transversely into disks, when they are subjected to chemical treatment. The rods

The Terminal Segments....

mm.), whereas the cones are usually shorter (.035 mm.) and thicker (.006 - .0075 mm.) and are conical in form. Upon the rods delicate longitudinal, as well as transverse markings can be observed. In both the rod and the

cone cells the terminal portion is morphologically and chemically distinct from the basal portion. The former cannot be stained by means of many histological reagents which give the latter a definite color. While the terminal segment is doubly refracting, the basal segment refracts singly. The two segments are separated from each other by a thin disk of transparent, highly refracting, material. The basal segment in the cone cells is much thicker than in the rod cells, but in both

The Basal Segments. is, in general, of circular cross-section, and bulges transversely. The portion of the basal segment nearest to the clear disk is—in both cells—strongly marked by longitudinal fibrils and is very powerfully refracting. This portion is much larger in the cone cells than in the rod cells and is distinctly ellipsoidal in shape. Centrally and continuous with the basal segment lies what we have termed the nuclear portion of the cell. In the rod cells this is composed of a very delicate fibre which expands in about the middle of its course, to embrace a large nucleus, and terminates in a small rounded enlargement. The nucleus of the cone cell is usually placed very close to the basal segment, is more oval in shape, and the fibre, which is of about the same length as the rod fibre, is very much stouter than the latter, and terminates in a ramifying "foot", instead of a knob. These nuclear segments of the rod and cone cells make up the so-called outer nuclear layer (6) (page 154), and they are in synaptic connection with the bipolar neurons of the outer nuclear layer (3).

The Pigmented Epithelium... The cells of the pigmented epithelium appear hexagonal in a tangential section of the retina, taken in the region of the epithelium. They possess
a large nucleus, and large number of pigment grains, which consist of crystals of a brownish substance to which Kühne gave the name fuscin. The longitudinal axes of these crystals are placed radially within the cells. The surface of the pigment cells which abuts upon the choroid coat of the eye is smooth, but the surface facing and in contact with the terminal segments of the rod and cone cells is provided with delicate filamentous processes containing the pigment; these processes—when the retina is stimulated, at least—partially occupy the spaces between the rods and cones. The average diameter of these cells is .012 to .018 millimeters, but they are smaller in the macula lutea.

The Nuclear Segments are not Concerned in Stimulation........... We have stated above that the independent light sensitivity of the fovea is proof that the point at which light energy changes into the energy of the visual impulse—the point of stimulation (cf. page 60)—does not lie within the five inner layers of the retina, if—as we have every reason for doing—we assume that the functions of these layers are essentially homogeneous throughout the retina. The seat of the transformation must, therefore, be located within one of the four regions the general contents of which we have above described. Since only cones are present in the fovea we may confine ourselves to a consideration of the properties of these, applying our results to the rods as well, if analogy does not chance to work against such an application. The light sensitive region, then, may conceivably be realized in any or all of the following divisions of the retina: (1) the nuclear segments of the cone-cells, (2) the basal segments of the cone cells, (3) the terminal segments of
the cone cells, (4) the cells of the pigment epithelium. As we have indicated above, it seems unlikely—from general considerations—that the first region is of importance, for the reason that it possess a form which does not depart radically from that of portions of any nerve cell. However, it has some peculiarities which distinguish it from the typical nerve cell fibre and perikaryon, and for that reason we could not eliminate it from the discussion if it were not for another fact. In the extra-foveal parts of the retina the axes of the cone (and rod) cells are rectilinear and are, in general, radially arranged with respect to the nodal point of the eye. But in the fovea the great majority of these cells are strongly curved, so that while the basal and terminal segments of the cells are still disposed radially, the nuclear portions make an average angle of forty-five degrees with the radius. Since the visual acuity in the fovea corresponds pretty accurately in magnitude with the diameter of the cone cell, response in this region cannot depend upon the functioning of any element which presents to the light a cross-section very much greater than that of the cone cell at right angles to its axis. Hence it cannot depend upon the functioning of the nuclear segments, since in the fovea these often present a stimulable area twenty or thirty times as great. It is possible to imagine, however, that only a limited region of each of these segments is stimulable, but the only evidences which we possess of a functional differentiation of the latter is given in the nuclei, and it is found that the nuclei are not disposed in a regular manner, but may lie one upon another or present vacant interstices. Similar remarks apply to the few cellular representatives of the inner nuclear layer.
(4) (page 154) which appear in the fovea. We turn then to a consideration of the possibilities of the basal and terminal segments of the cone cells, as well as those of the cells of the pigment epithelium, -- in the quest for the light sensitive structures.

A Fundamental Argument With Reference to the Position of the Stimulable Structures

It might have been pointed out in the beginning that since the nerve impulse liberated by the light is obviously conducted in a direction opposite to that in which the light passes through the retina, if we regard the function of the entire retinal structure to be that of visual response we should expect the nervously connected elements which are farthest away from the source of light to be those in which the impulse is aroused, for there are only two functions which need to be performed within the eye, one being the production of the impression, and the other being its conduction to the brain. In considering the actual structure of the eye we must admit that elements which are farther away from the light source than those by means of which the light initiates the impulse must either possess some function other than a purely nervous one, or must be useless. Since we doubt the presence of non-functional elements in the eye, we ought--other things being equal--to assume that the last retinal element to be reached by the light is that one upon which the stimulus directly acts. Since this element is obviously the cell of the pigment epithelium it seems advisable to consider carefully its claims to be the seat of visual stimulation.

The Most Probable Function of the Pigment Epithelium.

It will be recalled that Konig, Nicati, and Oppolzer placed at least a portion of the light sensitive chemicals the existence
of which was postulated by them, in the pigment epithelium. Now the probability of the complete validity of such an assumption cannot be estimated apart from an examination of the exact nature of the hypothesis involved. If the stimulation is supposed to depend upon electro-chemical reactions the view may be more acceptable than one which relies upon purely chemical conceptions. Let us, as a preliminary step, attempt to determine the functions which may reasonably be attributed to the pigment epithelium apart from that of a possible sensitivity to light. If it can be shown that the existence of this layer of the retina is explicable upon ground other than those of its alleged light-responsive character, we shall no longer find ourselves forced by our adoption of the evolutionary point of view to assume that it contains the stimulable elements.

It is self-evident that whatever else it may be the pigment epithelium is a non-bilation device, and that it acts in the same manner with respect to the retinal image as the black backing of a photographic plate or film with respect to the photographic image. Assuming for the nonce that the actual light sensitive elements are not contained within the pigment epithelium these elements, failing to absorb or reflect all of the light falling upon them, would transmit a certain amount of it to the back of the eye, from whence, if this latter region were of a non-absorbing character (not black) it would be reflected and thus confuse the image. The pigment epithelium not only acts beneficially in the absorption of light which has passed through the rest of the retina without being utilized, and thus makes it optically harmless, but the processes of the epithelial cells penetrate between the rods and cones and prevent these from becoming centers of
diffusion for the light which may be reflected or refracted from it, is important in the development of the photopic power of the eye, taking them as individual units. The arrangement of the long axes of the pigment crystals so that they are parallel with the axes of the rods and cones gives a maximum amount of absorbing surface for light reflected tangentially, from these elements (cf. page 159). It has been noticed that in cases of the disease of the pigment epithelium the visual acuity of the patient is very greatly diminished, images becoming blurred and indistinct. This fact has been used by Nicoli in support of his view that the pigment epithelium is the seat of stimulation, but it is probable that the real explanation is optical rather than chemical; the retina has lost its non-halation backing.

The Nutritional Function of the Pigment Epithelium Another disturbance which accompanies a pathological condition of the pigmented epithelium is that of night-blindness, or hemeralopia. Kühne in his experiments upon the properties of the visual purple showed that this pigment, which is found only in the rods—a fact which we shall later consider in detail—owes its formation to the action of the pigment epithelium. There is little doubt that one of the functions of this layer is the transmission of food—the basic substances necessary to the activity of the cells—to the elements of contiguous layers of the retina. The outer strata of the retina are not furnished with blood vessels, and especially in the fovea, where there are no vessels in any layer although the region is the most important one of the retina, the supply of nutritive substances must come from the choroid coat, which lies immediately external to the pigment epithelium. The large nucleus of the pigment cells may be taken as an indication of metabolic activity
and it is probable that much of the raw material of the blood which is to supply the remaining outer layer of the retina goes through its first stages of refinement in the pigment cells, which are capable of coming into intimate contact with the nervous elements. This holds, without doubt, for the rods, and the existence of a great accumulation of capillaries in the choroidal coat immediately opposite the fovea indicates that the cones may be nourished by a similar path. This nutritive function of the epithelium must, of course, be regarded as secondary to that of preventing retinal halation, and as more or less accidental in character.

The Cells of the Pigment Epithelium Are Too Large to Permit the Demonstrable Foveal Acuity. .

We see that the existence of the pigmented epithelium can be accounted for from an evolutionary standpoint by recognition of its obvious and very important function of maintaining the definition of the retinal image. But from this it does not immediately follow that it may not itself be the sensitive layer. One difficulty which already stands in the way of such a view, however, lies in the very nature of this protective function of the pigment. Most writers of textbooks of physiology regard the nature of the pigment epithelium as if it were mysterious; as a matter of fact there is no part of the eye the function of which is more patent. Why should the opaque epithelial cells so carefully surround the rods and cones if the latter are not the sensitive elements the excitations of which must be kept pure? Well, of course, it is possible that we have misinterpreted this intimacy of contact, and that the adaptation of the pigment cells to light absorption may not be for the purpose of destroying the light, but for that of changing (over)
1 J. Q. p. 246.

We see that the differences of...
it into the nerve impulse. However, definite reasons can be assigned for refusing to believe that the pigmented epithelium is the source of the visual impulse. In the first place, the pigmented layer has no direct nervous connections, and is not a nervous tissue, but is, on the contrary, a cuboidal epithelium which is developmentally discontinuous with the nervous layers of the retina, being the sole product of the outer wall of the embryonic optic cup. If the pigment cells are the light sensitive elements they must obviously generate the nerve impulse by a secondary stimulation of the rods and cones. A second objection to the view is found in the relation of the size of the pigment cells with the facts of visual acuity. It has already been said that our capacity to discriminate two retinal impressions as different is closely correlated with the size of the cones, and that the sensitive elements of the retina, whatever they are, cannot be larger than the cones. But the pigment cells cover, on the average, seven or eight times the area covered by a single cone. It should be noted, however, that they are smaller in the macula than elsewhere, and that they are capable of being regarded as individualized elements, since they are separated from each other by intracellular spaces of some magnitude. The diameter of the individual pigment cell in the macula is .010 mm., but the diameter of the cones in this region is also decreased, being only .002 mm., so that the ratio of the areas of the cones to that of the underlying pigment cells is as one to twenty-five. According to Helmholtz, the distance separating two images upon the retina which are just capable of being

separately perceived is about .0048 mm. More recent measure-
ments give still lower figures, but even upon Helmholtz' esti-
mate, the pigment cells are over five times too large to account
for the actual acuity. We have assumed in this argument
that if any portion of the cell is excited the whole of it is
excited. This might not be true for brief illuminations, but
with continued stimulation the chemical or electrical condition
holding in one portion of the cell would surely spread to the
others. Now those who assume that the cells of the pigment epi-
thelium are the seat of light-sensitive substances generally
believe that certain chemical changes take place in these cells
under the influence of light, and that the products of these
changes excite the rod and cone elements with the production
of the nerve impulse. So far as it is possible to see at present
all such ideas must be discarded on account of the fact that this
process would necessitate the simultaneous stimulation of four
or five cones by an element of light which, as experiment proves,
can stimulate only a single cone.

Further Analogies Detrimental to the Epithelium Hypothesis. Apart from the signifi-
the rods and cones in themselves, there are some further consid-
erations which tend to make it improbable that the pigmented epi-
thelium is of fundamental importance in the light response of the
retina. If the pigment epithelium were essential to visual-res-
ponse in any form, degeneration of this epithelium should lead
to total blindness. As a matter of fact it merely leads to im-
paired acuity, and hemeralopia, showing that the epithelium is
an auxilliary and not a prime actor. Furthermore, the induction

1 W.H.R.R., p. 1101. 2 Cf. STRATTON, G. M.: A New Deter-
of chemical changes outside of the rods and cones with resulting stimulation of the latter, a process which every upholder of the hypothesis of epithelial stimulability admits must follow the initial excitation, is a relatively crude and uneconomical process, and one against the acceptance of which as a representation of the truth of the case we are able to bring forward the analogy of the visual purple, which is certainly a light sensitive substance, and is found only in the peripheral segments of the rod cells, and so far as we know does not exist in the pigment cells, although the presence of these is essential to its formation.

König, it will be recalled (cf. page 128), believes in the efficacy of the visual purple as a cause of sensations of white and blue, but places the substances inducing green and red within the pigment epithelium. His hypothesis as to the nature of the cones makes the latter optical devices for concentrating the light upon the epithelium. But it is impossible to imagine any advantage which could arise from such a focusing process. The acting elements of the epithelium are much larger than the cones. The alleged concentration of the light by the cones (and it seems likely that there actually is an effect of this sort) could not increase the effectiveness of the radiant energy as a stimulus; the same amount of light would act upon the cell whether it were concentrated or not (segregated or not), and the same amount of chemical change would be induced. An explanation—such as this one of König's—which is contrary to the evolutionary principle that every existing organic mechanism must possess
utility, cannot be accepted. Both the cones and the epithelium must possess some other function.

The Difficulty of Imagining the Mode of Transference of stimulation from Epithelium to Rod or Cone. Even if we discard the results of the above argument and assume that the initial stimulation effect is produced upon the epithelium, we have still the difficulty of explaining the manner in which the cones or rods are excited in turn. A. Pizon (cf. page 125) believes that the light sets up a mechanical vibration in the fuscin crystals (cf. page 159), and that the stimulus to the rods and cones is a literal battering, a mechanical reaction. H. M. Bernard (cf. page 126) holds that the pressure exerted by the epithelium upon the ends of the rod and cone cells is the cause of the visual impulse. We shall criticize these and other mechanical hypotheses further on. According to W. Nicati (cf. page 138), the secondary stimulus given to the rods and cones is electrical. This seems hardly more than a euphemistic way of admitting that we do not understand the process. König fails to be explicit. The rods and cones are separated from the pigment cells by a continuous membrane (cf. page 157), which may permit a relatively slow diffusion of nutritive substances, but would probably offer high resistance to any chemical transference process acting with the velocity of the visual response.

Merits of the Outer Segments of the Cone and Rod Cells for Stimulation. Thus it appears advisable, at the present point in our discussion to reject the view that the pigment epithelium is the seat of the process of visual stimulation, and to turn our attention to the remaining elements of the outer receiving surface.
tina, viz., the peripheral and basal segments of the rod and cone cells. If it is assumed that within these bodies is to be found the complete mechanism underlying the retinal sensitivity to light we immediately have an explanation of the relations which exist between them and the epithelium, as well as of the existence of the epithelium itself. This we have already made clear. We may also readily perceive the meaning of these extremely specialized structures in themselves.

We have seen that the basal segments of the rod and cone cells may be divided into two regions (cf. page 158), one—outermost—which is heavily fibrillated and powerfully refracting and the other—innermost—made of a clear, homogeneous, material. The highly refracting portion is ovoidal in form and so arranged that its axis coincides with that of the cell. In some of the lower animals this structure is even more characteristically lens-like than in man, and is known as the "ellipsoid." Its obvious function is the concentration of the light upon the external rod and cone segments. Although there is no reason for believing that such a concentration of light would be advantageous in connection with a stimulability of the pigment cells, there is every reason to suppose that it would be of advantage if the external segments—rods and cones—of the rod and cone cells are light sensitive, since these elements, especially the cones—are appreciably smaller than the adjacent basal segments and, like the pigment cells, are not packed closely in contact with one another. In the fovea the cone bases form a mosaic made up of hexagonal elements, and thus present to the light an unbroken absorbing surface, but the cones themselves (the terminal and outer
segments) are still separated by an intercellular space which, as we have seen, is partially occupied by the processes of the pigment cells. If we assume that these terminal cone (and rod) segments are those actually acted upon by the light we perceive that the arrangement described above is an ideal one for clear and powerful impression. It is desirable that the sensitive elements should be insulated from each other in order that the response of one may not prove a stimulus to that of an adjoining one, either on account of its becoming a source of physical or of chemical disturbances. Hence we find these elements smaller than the basal segments, and separated by the intracellular space and the pigment processes. But the loss of impinging light which this insulating structure tends to bring about is compensated by the optical system of the basal segments. All of the light which falls upon these segments will be split up by the highly refracting lentiform ellipsoids into an immense number of microscopic beams each having an intensity higher than that of the originally impinging rays. Thus all of the initial light energy will be conserved. In the human fovea centralis the extreme crowding of the cones, brought about in the interests of increased acuity, has reduced these optical structures to a more or less vestigial state.

The ellipsoidal region of the basal segment is obviously made of a specialized protoplasm. Since if the nerve impulse is actually aroused in the external segments it must pass through this region, one might anticipate that the specialization of the latter for refraction might lead to non-adaptation to nervous conduction. Now we have some reason for believing that the fibrils which are to be observed in continuous lengths within other characters can be further considered.
any nerve fibre are the actual conducting elements. In this case we may explain the fibrillation of the ellipsoids by assuming that this latter phenomenon represents the conservation of the mechanism of nervous conduction in the face of the optical differentiation. No fibrils have been observed in the inner portion of the segment, but the nuclear and obviously conducting segment in the case of the cone cells is strongly fibrillated. The thin clear "intermediary disk" (cf. page 156) which separates the internal from the basal segments is probably to be interpreted as a portion of the optical system of which the ellipsoid is the most obvious element. The ellipsoid is a condensing lens, the intermediary disk a collimator.

The Terminal Segments of the Rod and Cone Cells are the Regions of Stimulation.....

It is believed that the above interpretation of the structure of the basal segments of the rod and cone cells will, if accepted, make it manifest that the external segments of these cells are those which are concerned in the actual generation of the visual impulse. The fact that they are the nervous connected elements which are farthest from the light source, their specialized structure, their physiological and optical isolation, their rigid parallelism with the rays of light, the apparent concentration of radiation upon them by the ellipsoids of the inner segments, and--finally--the fact that in the case of the rods a known light-sensitive substance--the visual purple--is present, --all lend support to the hypothesis that these rod and cone segments are the actual seats of visual stimulation. We shall see at a later point that their attribute of double refractivity--and other characteristics--lends further aid to this view of their
function.


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Section XIX: The Problem of the Specific Nature of the Process of Visual Stimulation.

Chapter 8: The Action of Light Upon Matter and the Principle of Resonance.

All Physical Explanations Must Be Electrical At Bottom.

We have seen that hypotheses concerning the manner in which light induces visual sensation can be roughly divided into three classes (cf. page 123), the mechanical hypotheses, the chemical and the electrical. It now behooves us to examine the relative merits of these different points of view. In the first place we must clearly recognize the relation which exists between mechanical, chemical and electrical explanations of phenomena. The three are far from being mutually exclusive, as we have already observed in our review of the several current hypotheses. In the present state of development of physical science it seems likely that all physical hypotheses (explanations) may ultimately be expressed in terms of electrical variables. An electrical explanation of any phenomenon is probably the most fundamental explanation of it which can possibly be given, apart from a metaphysical analysis; it seems likely that a complete account of the universe in physical terms—when ultimately given—will be expressed in a finished theory of the dynamics of electrical particles; this will be the theory of nature. Chemistry and Newtonian mechanics will then be departments of electro-dynamics which deal with electrical systems of two successive stages of complexity, namely those represented in the atoms and the molecules which—in the physical sense—make up matter, and secondly, the molecular aggregates which constitute
ponderable bodies, or—as we say—molar as opposed to molecular and sub-molecular quantities. An account of the mechanism of visual sensitivity which pretended to be physically complete and exhaustive, therefore, would necessarily be in the form of an electrical theory, and the underlying hypotheses would be completely electrical mechanisms. Such an account cannot be given at the present time, because of the incompleteness of our physical ideas, and would at any stage of development be superfluous for the reason that most of the processes involved could be adequately expressed in terms of the particular properties of special electrical aggregates, atoms, molecules, or molar masses of matter. In connection with these, however, we may often be forced to deal with the properties of electricity in general. To sum up, a thorough description of all of the physical elements of the process of visual response would necessarily be a description of an electrical hypothesis, but a proximate description can presumably be given in terms of those properties of electrical aggregates which are studied in chemistry and molar physics, with only slight use of the fundamental conceptions of electrodynamics.

Light Acts Electrically to Produce Chemical Effects.

In a sense the distinction between the mechanical, the chemical and the electrical is merely one of degree of refinement; in the processes of vision we may be concerned with the activity of free electrical charges, or with that of atoms and molecules (which we imagine to be complexes of such charges) or with that of bodies, which we regard as compounds of atoms and molecules; in the first case our problem will be purely electri-
ocal, in the last two cases it would be electrical at bottom, but could be discussed in chemical or mechanical terms, without much reference to the final electrical meaning of these terms. It is believed that upon this basis we can demonstrate without much difficulty that the underlying mechanism of visual sensitivity is predominantly chemical, and that the electrical elements which are involved are of much greater importance than those which are mechanical. We have already described the nature of the visual stimulus (page 147). It is wholly electrical in character; light is moving electrical energy. As such it is capable of acting only upon electrical systems and it follows that if we are to postulate the existence of a light-responsive structure within the eye we must admit at the outset that that structure contains electrical charges as one of its essential constituents. This necessity need not annoy us, since if we regard the light perceiving (sic) structures as material, we of necessity regard them as containing both positive and negative electricity. It is requisite, however, that this electricity be in such a form that the light can act upon it effectually with the production of some change which can result in the visual impulse.

The Chemical Dynamics of Light

We have said (cf. page 148) that whenever a ray of light passes through a fixed point in space there is a rapid oscillation of electrical and magnetic forces at this point, the frequency of these oscillations being that of the light, and proportional to the light velocity and the reciprocal of the wave-length of the light. These forces are exerted at right angles to the direction of motion of the light and at right angles to each other. If the ray is absorbed or reflected there is also a mechanical force, the
so-called light pressure which operates in the direction of impact of the ray. Now an electrical force is simply a tendency towards the acceleration of an electrical particle—so far as the particle is regarded as stationary—while a magnetic force is merely a similar tendency towards the acceleration of a moving electrical particle at right angles to its line of motion. It follows that when light passes through any region of space containing electrical charges these charges will be disturbed both as regards position and as regards motion—if they are already moving—and that this disturbance will be oscillatory in character. Now we suppose the atoms of matter to be made up of positive and negative charges, about evenly balanced in magnitude, so that as a whole, particular atoms are approximately neutral electrically. Any electrical force tends to accelerate positive and negative charges in opposite direction, so that it can be seen that if an electrical force were to act upon a compound of positive and negative electricities it would tend to break up the compound by thrusting its components in opposite directions. However, since the energy of light is very small compared with the intra-atomic energies, we should hardly expect a decomposition of the atom under optical stimulus, although we do find that light is able to liberate electrons from metals (in which, however, some of the electrons are not closely bound to the atom). But it is a well known fact that atoms themselves may bear electrical charges—over and above their intrinsic electricities—and that many chemical compounds can be regarded as made up of two or more components, one or more of which are electro-positive, the other or others being electro-negative. It is only when these components separate from each other that their electrical nature becomes obvious, since within the mole-
cule—as within the atom—the electricities are approximately balanced. When liberated in this way they are called ions, but we have every reason for believing that the ionic condition is the outcome of their mode of combination within the molecule. Now if a molecule the component atoms or atom-groups (radicles) of which bear opposite charges is acted upon by an electrical force these components will tend to separate and to move in opposite directions. Something like this is what occurs in electrical conduction through liquids and gases, as in the galvanic cell and in discharges through vacuo. Light waves passing through a molecule of this sort would tend to separate it into its two component ions, and since the internal energies of many chemical substances are very small it is not unreasonable to expect that in certain cases light will actually bring about chemical decomposition. Under proper conditions chemical synthesis, also, may be brought about by the action of light, if this tendency to strain the internal bonds of certain molecules results—after the manner of catalysts—in the production of molecular conditions more favorable to special chemical reactions.

Consequence of the Oscillatory Character of Light But the electrical forces which constitute a light vibration are not simple constant tendencies; they are forces which are changing in magnitude and sense (+ and - direction) at every instance. Now only this, but the total effect in one direction throughout any time is exactly equal to the total effect in the opposite direction, if an integral number of cycles is passed through in that time. The spectral light which induces the sensation attribute of redness (the slowest vibration) changes
the direction of the electrical forces acting on account of it at a fixed point in space approximately $4 \times 10^{14}$ or four hundred million million times per second. The effect of such a rapid reversal of forces would obviously be dynamical neutralization; the light first pushes in one direction, and then, for an equal time and with equal intensity pushes in the opposite direction. Unless the masses upon which the force acts are exceedingly quick to respond, the displacement which occurs will be infinitesimal and whatever it is, it will be immediately negated by the subsequent equal push in the other direction.

The Principle of Resonance..... There are certain conditions under which this neutralizing tendency will not take effect, and a study of the nature of these conditions will immediately disprove all hypotheses of vision which depend upon a supposition of the existence of mechanical vibratory response to the oscillations which constitute light. Any displaceable particle when acted upon by a periodically varying force will vibrate in synchronism with the variation of that force. The amplitude of these vibrations will depend upon the intensity and time of action in a uniform sense of the disturbing force, the magnitude of the restoring force, and the inertia of the particle. If the particle has a relatively large mass and if the disturbing forces are weak and of high frequency—as in the case of light—the amplitude of vibration will be very small, and in general will be constant in magnitude if the forces are constant. However, there is a certain special condition in the fulfillment of which the amplitude of the vibrations may increase indefinitely without change in the intensity of the disturbing forces. If
a particle is normally acted upon by balanced forces in such a way that any displacement of the particle means destruction of the equilibrium involved, so that it tends to return once more to the neutral position, this particle will possess what is known as a natural period of oscillation, and after any displacement it will oscillate in this period about its neutral point until radiation of energy finally brings it to rest. The pendulum bob may be presented as an example of a body governed by a law of this sort. Now if such a particle be acted upon by a periodically varying force the frequency of which is the same as—or very similar to—the natural frequency of the particle itself, the amplitude of the oscillations set up in the particle will increase with the time, energy being absorbed and stored up in the natural vibrations. This gives rise to the phenomenon known as resonance, which is important in acoustics and also, it appears, in optics. Dynamical systems of the right dimensions are capable of storing up energy under the influence of forces oscillating with a particular frequency, but not with others; needless to say, this frequency is approximate, not critical, except when we desire to postulate an indefinite and permanent increase in amplitude of vibration on the part of the reacting particle, in which case the period of the disturbing force must be exactly that of the particle itself when in natural vibration. We shall find this principle of resonance of much importance in our criticism of current hypotheses concerning the nervous mechanism underlying visual sensation.

1 RAYLEIGH, J. W.: Theory of Sound; 2nd ed. (1894); i, sec. 46.
Chapter 9: A Criticism of Mechanical Hypotheses of Visual Stimulation.

Nearly every hypothesis of the mechanism of selective visual stimulation by light of different wave-lengths is based upon the principle of resonance the exposition of which we have just completed. Young apparently had phenomena of this sort clearly in mind when he propounded his original theory of vibrating particles. It is the explicit basis of Mrs. Ladd-Franklin's molecular theory and figures prominently in the mechanical hypotheses of A. Pizon, Stöhr, Patten and others (cf. page 124). None of them, however, have paid attention to the mathematical aspect of resonance, and thus—at least in certain cases—have been led to absurd conclusions concerning its applicability. We refer especially to the mechanical hypotheses.

A Mathematical Refutation of Mechanical Hypotheses. In all naturally oscillating systems the restoring force for small displacements follows Hooke's law, and is thus proportional to the magnitude of the displacement. Under these conditions the frequency of vibration, \( n \), is proportional to the square root of the quotient of the mass of the vibrating particle into a certain constant: \( n^2 = \frac{k}{m} \), where the restoring force is \( F = kx = ma \), where \( x \) is the displacement. Now a maximum of resonance is possible only when the natural frequency, \( n \), of the resonating system is equal to that of the disturbing force. As we have said, the minimum frequency for visible rays is that of the light inducing the sensation attribute of red, about \( 4 \times 10^{14} \).

This formula involves the neglect of a factor of \(4 \pi^2 = (\text{approx.}) 40\). Calculated on the basis of the more exact formula, the final expression for \(Y\) (page 183) is

\[
Y = \frac{4 \pi^2 k^2 M L}{\lambda^2 a} \quad \text{where } -W_{\text{xx}} = \text{the force on the particle. For light of } \lambda = 750, \text{ this formula gives } Y = 17 \times 10^{21}.
\]
cycles per second. If, for complete resonance, we write: $n^2 = (4 \times 10^{14})^2 = K/m$, we have $K/m = 16 \times 10^{28}$, that is, in order that a system should possess the power to resonate with a light of wave length $\lambda = 750 \mu \mu \mu$, the ratio of the restoring force to the displacement divided by the mass of the particle must be equal to $16 \times 10^{28}$. This implies either a very small mass or a very large coefficient $K$. If we assume that the vibrating particle is of such a size as to be visible under the microscope we may not make use of a diameter less than $0.004 \mu \mu = 4 \times 10^{-7}$ cms., which is that of the smallest particle visible under the ultra-microscope. Assuming this particle to be a sphere and of specific gravity unity, its mass becomes $m = \frac{4}{3} \pi (2 \times 10^{-7})^3 = 4 \times 8 \times 10^{-21} \times 3.1416/3 = (\text{approx.}) 32 \times 10^{-21}$. Substituting this value in the above equation, we have for $K$, $K = 16 \times 10^{28} \times 32 \times 10^{-21} = (\text{approx.}) 5 \times 10^{9}$. On the basis of this datum we can calculate the modulus of elasticity of the substance acting in the restoring process: $Y = (5 \times 10^9 \times \pi \times L)/\pi \times (0.002 \times 10^{-4})^2 = L(5 \times 10^9)/(3.14 \times 4 \times 10^{-14}) = (\text{approx.}) 4 \times 10^{22} \times L$. $L$ is the length of the column of active material. This cannot be greater than the diameter of a retinal cell, say $10 \mu = 10^{-2}$ cms., so that $Y = 4 \times 10^{20}$, a modulus of elasticity $2 \times 10^8$ = two hundred million times greater than that of hard drawn steel. The conclusion is obviously equivalent to a reductio ad absurdum of the theory of mechanical visual stimulation, provided in such theory recourse is had to the principle of resonance. The elasticity of any substances which we can reasonably suppose to exist in the retina of the eye cannot even approach that of metals, to say nothing of exceeding it by such an enormous factor, and the meaning of this

result for our discussion is obviously the discrediting of all mechanical hypotheses of visual stimulation which rest upon an application of the principle of resonance.

Further Objections to Mechanical Hypotheses

Unless the material particles which are supposed—in these mechanical hypotheses—to vibrate in unison with the light-waves bear definite electrical charges (as do colloidal particles) the only basis for response would be that of light pressure. But this is not a periodic force. Professor Patten has emphasized the fact that the retinidial fibrils (cf. page 125) the presence of which he has noted in the visual cells of certain animals, are always arranged at right angles to the path of the light rays. This arrangement is just the reverse of what would be desirable if the response of the fibres was to be of a mechanical nature, depending upon the reaction of the electrical forces of the light with the possible charged colloidal particles adsorbed upon the fibrils, since the electrical forces operate only at right angles to the path of movement of the ray. Light pressure, however, is exerted in the direction of the ray, and is dependent only upon reflection or absorption, not upon unbalanced states of electrification; but this is a force which does not lend itself to the production of resonance phenomena.

All of these forces, it must be realized, are very small in magnitude and even if it were possible to conceive of a protoplasmic fibril which could resonate with them if it were suspended in free space, it is impossible to conceive such resonance when, as is the actual state of affairs, they are surrounded by viscous liquids which introduce a large element of friction. Resonance, that selective response to special frequencies of vibration upon which all hypotheses of the
mechanism of visual response must finally be based, is inseparably bound up with the capacity of the resonating system to absorb the energy of the stimulating agent, and to store it up in the form of active oscillations. This capacity does not exist in the presence of powerful frictional resistances, such as would be present when a fibril oscillates within the body of a protoplasmic fluid.

Explanation of the Retinidial Fibrils

Patten, it is true—in a few sentences at the conclusion of his paper—admits the difficulties of the mechanical view with regard to the action of the retinidial fibrils, and suggests that they may respond with electrical oscillations, the resonance being of the sort well known in connection with selective receiving instruments in wireless telegraphy. We shall find, however, that this also is an untenable hypothesis, especially in the form in which it is put by Patten. It is probable that the so-called fibrils noticed by the observer are not fibrils at all, but are artifacts representing the surfaces and lines of junction of the little disks and sectors into which the sensitive elements of the visual cells are divided. Under certain conditions of staining, these might very easily assume the appearance of definite structures, owing to the deposition of the staining material along the lines and surfaces of contact; similar effects are common in histological work upon other tissues. The use of high powers in magnification is very conducive to an illusory character in the microscopist's perceptions; even in Professor Patten's original (non-diagrammatic) drawings, the so-called fibrils are by no means convincing-ly clear cut structures.
Interpretation of Pizon's Observations

We may consider that the above discussion disposes finally of all hypotheses of visual stimulation which depend upon the resonance of mechanical (that is: molar) systems to light. We have paid special attention to Patten's theory because it is the most definitely expressed conception of its kind, but the results apply equally to the theories of Pizon, Stohr, Charpentier, and the older "three fibre" theory which arose as an interpretation of Young's hypothesis. Pizon bases his hypothesis upon certain vibratory movements which he has actually observed in the pigment granules of the eyes of some of the lower animals. These vibrations were no doubt due to the slight temperature differences which always exist in small volumes, giving rise to the phenomenon commonly known as the "Brownian movement." It is certain that a vibration corresponding with that of light could not be observed as such, on account of its almost unthinkable rapidity. On the other hand slow vibrations induced by temperature changes incident upon the absorption of light cannot be made the basis of a theory of selective response without the concomitant introduction of molecular factors.
Chapter 10: The Conception of a Molecular Resonator and its Relation With the Structure of the Rods and Cones.

Intra-atomic Resonance...

Of course the mathematical reasoning which has led us to discard mechanical hypotheses of visual stimulation cannot be presented as a detailed examination of the conditions of that stimulation, but it is none-the-less conclusive, since it shows that the mechanism concerned belongs in a different class, is of a different order of magnitude, from that of molar systems of even ultra-microscopic dimensions. This, of course, is a fact which must be immediately obvious to every follower of modern physical speculation. If we are to explain the facts of selective response to lights of different wave-lengths by use of the principle of resonance—and there is no other satisfactory way in which it can be done—and if we are acquainted with the origin of the periodic forces with which the visual apparatus is considered to be in tune, we must of course assume that this apparatus, so far as it resonates, is of the same general order of magnitude as the mechanism which gives rise in the beginning to the periodic force. Now we have seen (cf. page 150) that light is the outcome of the oscillations of electrical charges and cannot be regarded as producible in any other way. There seems to be little doubt, from the standpoint of modern physical assumptions and their consequences, that the charges which are concerned in the production of light are those which—in part at least—constitute the atoms of matter. The electrical theory of matter assumes that the elementary atoms are made up of positive and negative electricity in about even-
ly balanced quantities. The positive electricity is in the form of a large sphere which may be of various sizes in different elements, but the negative electricity is all within the atom as electrons, which are the ultimate units of negative electricity, having a definite mass (1/1700 that of the hydrogen atom) and a definite charge. If the electrical hypothesis is valid we must admit that there are thousands of electrons within each atom of the heavier elements. It is supposed that these electrons are arranged in systems which are in motion—perhaps in rings, after the manner of the swarming satellites of the planet Saturn—and in dynamical equilibrium. Such an electronic system when disturbed will oscillate in its own natural period and will give out radiation of corresponding frequency. A study of the relations existing between the spectra of different elements and between the parts of the spectra of the same element make it almost certain that this account of the origin of light radiation is physically correct. The fact that certain of the spectral lines (frequencies of light emitted) of single elements are arranged according to definite laws suggests that the same electronic system within the atom may possess several natural frequencies, as is the case with a piano string; in this event, the system would resonate with several distinct lights.

Intra-molecular Resonators... We have suggested above a process in accordance with which it is conceivable that light should produce chemical change (page 176), namely by the pulling apart of two ionic components of a molecule. But if we are to have a selective response—and this is essential for a chemical theory of visual stimulation—these ionic components must possess natural periods of vibration within the mole-
cule such that the incidence of the light ray upon the latter will set up tuned oscillations which, increasing in magnitude, with the absorption of the light energy, finally result in the bursting of the atomic bonds. Now it appears, from what we have said above, that in general light radiation is set up by intra-atomic rather than inter-atomic activity, so that we should not anticipate a sensitivity of the ionic parts of the molecule to light vibrations. Molecular masses seem still too large and chemical forces too weak to permit the high frequency of oscillation which is requisite to resonance with light. The characteristic absorption bands of chemical compounds such as haemoglobin or potassium permanganate, however, indicate that this process may actually take place. These absorption bands which are exhibited by chemical compounds are not obviously derived from the absorption bands of the elements composing the compounds; they are much broader than the bands produced by the elements and are differently placed in different compounds of the same element. It is possible that the absorption bands of compounds are dependent upon the relations existing between special electronic systems within the atoms and the larger system of the molecule itself, so that a path is formed by which light energy absorbed by the resonating intra-atomic systems is transferred to the molecule as a whole to result in chemical change of in radiation at a lower frequency (heat waves). The different internal structures of different compounds would thus determine different absorption spectra even with the same fundamental elements. These problems are still being debated by the physicists and we shall here make the simpler assumption, namely that (over)

the atoms or radicles within a compound possess natural frequen-
cies of their own which are of the order of those of light.
This assumption is not unreasonable, since the electronic sys-
tems of the atom are presumably not of a very different order
of magnitude than the atoms themselves, and while we know that
the energies, and hence the ultimate forces within the atom are
vastly greater than those of the molecule—tending, therefore,
towards much higher frequencies—it is far from probable that
these ultimate forces are those acting in the maintenance of
the equilibrium of the electron systems as parts of the atom; it
is only when—as in the case of radioactivity—some of these
systems break away altogether from the sphere of positive elec-
tricity that the energies and forces involved become so prodig-
gious. In order that the elements of a compound should respond
to light it is of course necessary upon this hypothesis that
they possess inherent differences in electrical charge, in short,
that they be actually or potentially ions. The effect of light
upon the compound would thus be that of ionic dissociation or
ionization. It is well known that ionization processes do occur
under the influence of light, although it is not certain that
the mechanism is that here assumed.

Let us call the light sensitive
molecules which have been postulated
above, molecular resonators, and let us
designate any such resonator by \( M_\lambda \), where \( \lambda \) is the wave-length
of light corresponding with the natural vibratory frequency
of the molecule. Each one of these light sensitive molecules
we imagine to be made up of two oppositely charged components
which, when liberated, are the ions \( I_+ \) and \( I_- \), the reaction induced by the light being \( M \rightarrow I_+ + I_- \). This is a simple chemical dissociation. Now within the molecule these ionic radicles will be capable of vibrating about their mutual center of mass, and when acted upon by light with which they can resonate they will absorb the radiant energy and the amplitude of the oscillations will increase until the two radicles are separated beyond the action of their mutual affinities, and thus drift off alone. Concerning the fate of these dissociated ions we shall have something to say when we come to consider the problem of the nature of the visual impulse. In a later chapter we shall also discuss the question of the probable number of specific molecular resonators present in the retina. Finally we shall be obliged to attempt a determination of the natural periods of oscillation of these resonators, as well as their chemical characters. Each postulated molecular resonator obviously necessitates the presence in the retina of a specific chemical substance. Concerning the relation of these substances with the retinal histology we shall now have something to say.

Explanation of the Double Refractivity of the Rods and Cones,..............

We have already noted the fact that the external segments of the rods and cones are divided up into minute disks and are doubly refractive to light. These facts immediately suggest a crystalline or crystalloidal structure, that is, a specific orientation of the component molecules which make up the substance of the rods and cones. That such a structure should exist follows from a theory of chemical stimulability, such as the one above outlined, a theory which differs from many
already current only in definiteness. The rod and cone segments are placed parallel to the path of the light rays, and for this reason the electrical forces of the rays must act within the segments at right angles to their axes. Now there are two general ways in which the molecular resonators might be distributed within the rod and cone segments; they might be distributed at random with their polar axes pointing in all possible directions and capable of being rotated in the heat vibrations of the substance, or they might be rigidly arranged so that their axes all pointed in a uniform direction. It is easy to see that only the latter arrangement would give a maximum responsiveness to light, since the electrical forces always oscillate in a plane at right angles to the axes of the segments, and only when the polar axes of all of the resonators were rigidly fixed in the same direction would their resonance be maximal. This follows from a simple resolution of forces. But a special rigid arrangement of the molecules of a body in this way corresponds with the crystalline state or with some condition of strain, and these are the only conditions under which we find a double refraction of light. The degree of double refraction depends, of course, upon the exact nature of the crystal; in crystals it is zero, while in others it is high. The tendency shown by the rod and cone segments to break up into disks is also a corollary of their crystalloid structure, as it is well known that crystalline bodies tend to split along planes bearing a definite relation to their axes, or, when large, appear to be made up of a number of smaller and symmetrical crystals.

To the above explanation of the physical properties of
Aesthesogenases the rods and cones it may be objected that these elements cannot be regarded as being made up of the light sensitive substances in themselves, especially after they have gone through a process of histological preparation. This fact is, of course, obvious, but it does not destroy the force of our explanation. It is clear that the molecular resonators, if broken up by light must be replaced by the constant manufacture of new molecules. This construction no doubt occurs in the rods and cones themselves and must be attributed to the presence therein of appropriate enzymes which regulate the reactions of the food material furnished by the blood. We believe that enzyme action is dependent not only upon a definite relationship between the enzyme and its substrate (enzyme and substrate being compared by Emil Fischer to key and lock) but also that in all enzyme action there is at some stage of the process a combination of enzyme and substrate and hence of the enzyme and its products. The application of these principles to our problem are obvious. The primary crystalloid substance of the rod and cone segments is that of the enzyme which catalyzes the light sensitive compounds from the lymph which must also be present. The definite orientation of the enzyme serves to fix that of the molecular resonators which are produced in intimate geometrical relationship with it. We may call the enzymes of the visual substances aesthesogenases—the enzymes of the sensation producers—and their substrates may be known as aesthesogens. It seems probable that the aesthesogens of the rods are derived directly from the pigment epithelium (cf. page 163) while those of the cones are partially prepared by the cone cell itself,
since the cone cell nucleus—the nucleus always being active in
the cell metabolism—is much nearer the cone segment than that
of the rod cell is to the rod segment.

Conjectures Concerning the
Meaning of the Conical ...
Forms of the Cones........

We may now inquire whether
or not it is possible upon our
present basis of discussion, to
give an explanation of the structural difference which exists
between the rods and the cones. As we shall see later,
there are reasons for thinking that the rods contain but a sin-
gle molecular resonator, namely, the visual purple. In discuss-
ing the properties of the cones, however, we shall be obliged
to postulate the existence in these retinal elements of three
or four such resonators. Since these must be different chemi-
cally, their enzymes must be different, and since for the pro-
duction of a crystalline structure relative purity of substance
is essential we should expect to find the different aesthesogen-
ases and their corresponding resonators at separate levels of
the cone segments. Difference in the molecular nature of these
might very well produce differences in the size of the various
crystalloid disks in which case, for architectural reasons, we
should expect the largest disks to be basal, the smallest api-
cal. But another explanation is possible. We have seen that
the so-called ellipsoid (cf. page 169) of the cone cells is
much larger than that of the rod cells. We have regarded it
as a structure which functions as a condenser of light, the in-
termediary disk which separates the external and middle segments
(terminal and basal segments) being held to act as a collimator,
which makes the rays parallel once more. Now we may suppose
this collimation to be perfect in the rods, but in the cones, on account of the effort to concentrate a greater amount of light the condenser has increased in power out of proportion to that of the collimator so that the rays, after passing the intermediary disk do not form parallel lines, but converge towards a point. This converging pencil coincides with the form of the cone. In the fovea, where the basal segments of the cones are compressed, the terminal segments are much longer than elsewhere and less conical, as upon this hypothesis we should be led to expect. Since the light rays of different wave-length differ markedly in refrangibility, the more refrangible—the "violet"—would come to a focus nearer the base of the cone than the less refrangible—e.g., the "red." It would thus be relatively more desirable that the molecular resonators be arranged so that those responding to the more refrangible lights should be nearer the base of the cone than those responding to the less refrangible lights. This corresponds well with the results obtained by König and Zumft in their efforts to determine the position of the retinal layers sensitive to lights of different wave-length. Using the method of shadows already described (page 155) they found that the sensitive layer appeared to be deeper the greater the wave-length, i.e., the less the refrangibility. However, the present writer believes that these results are due to the chromatic aberration of the proper lens system of the eye, and does not regard them as a proof of special arrangement of the molecular resonators in the cones as an adaptation to the chromatic aberration of the cone ellipsoid.

Chapter  : A Brief Criticism of Electrical Hypotheses of Stimulation.

Certain Vague Conceptions of Electrical Stimulation Having discussed the fundamental of a chemical hypothesis of visual stimulation, we may now briefly consider the value of certain vaguely formulated electrical theories of this process. We have seen that, at bottom, all hypothesis of vision must make use of the conception of electricity, since light is an electromagnetic energy and can act only upon electrical systems. But there are certain current visual hypotheses which postulate electrical effects which are not obviously simply deeper interpretations of chemical or mechanical processes. According to our conception of the final result of the action of light upon the retina, a certain number of characteristic ions are liberated. Of these there are equal numbers of positive and negative. Now Edridge-Green and others have assumed that a decomposition of the visual purple—or analogous substances—takes place under the influence of light in proximity with the cones (or rods), and that this process results in an electrical excitation of the latter. Such a stimulation is inconceivable apart from a special sensitivity on the parts of the cones (or rods) to the presence of positive or negative ions, a sensitivity which might be either chemical or physical in nature. Light could not produce any appreciable differences of potential in the region of the rods and cones apart from some mechanism more elaborate than the simple production of an equal number of positive and negative ions. It is probable that the authors mentioned above imply the existence of such a mechanism, but it is important to
notice that the electrical stimulation of nerves—as carried
on experimentally in the physiological laboratory—depends upon
sudden changes in the potential gradient along the axis of the
nerve, and that no simple ionization process—the only conceiva-
ble electro-chemical result of the action of light—can account
for any such changes in potential. In order that this potential
difference should be produced there must be present some machin-
ery which carries one of the ions—or its charge—off bodily,
and in such a way that the potential constantly increases during
the period of stimulation. In accordance with the law of Du
Bois-Reymond, the electrical stimulation of a nerve is dependent
upon changes in potential.

In addition to these electro-
chemical hypotheses we may mention
such views as that expressed by

Patten in the latter part of the paper which we have reviewed
(vide page 125). It will be recalled that he compared the little
loop-shaped retinal fibres which he had observed in the visual
cells of certain animals to Hertz resonators, conceiving the
response of these fibres to the light to be due to that species
of electrical resonance which is exemplified in a tuned wire-
less receiving instrument. It is, of course, true that light
waves would set up an oscillatory current in a circuit of the
proper dimensions, and containing free electrons. But we have
no reason for believing that the proper conditions for such reso-
nance exist outside of metallic conductors; only in such con-
ductors are there unbound electrons which are freely displace-
sable. But even if we suppose that the construction of such a
resonating circuit from protoplasmic materials is conceivable, it is none-the-less impossible that the oscillations thus produced should be conveyed along the nerve in any such way as that imagined by Patten, who assumes that similar constructions which he discovers in the visual brain centers also resonate in response to the afferent nerve impulse. As a matter of fact, nervous tissue is absolutely insensitive to continuous vibrations of any sort which have a frequency greater than twenty thousand per second. Oscillations of \(200,000,000,000\) per second could certainly not be transmitted along any neural conductor; both the differential sensibility in time and the related speed of conduction in space are too small.

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Chapter 12: A Proof of the Presence in the Retina of at Least Three Different Molecular Resonators.

The Facts Necessitating the Postulation of a Single Molecular Resonator............ One of the fundamental problems facing those who advance hypotheses concerning the neural mechanism underlying visual sensation is a determination of the number and specific sensitivity of the so-called fundamental excitabilities. Attempts to arrive at conclusions in this field have usually been based upon the results of "color-mixture" experiments, but in the following argument—in which we shall consider fundamental excitabilities to be equivalent to specific molecular resonators—we shall show that the dependency of the hue of the elementary sensation upon the wave-length of its inducing light and the existence of complementary lights in themselves necessitate at least three such resonators. Upon the basis of a special hypothesis with regard to the cause of complementation we shall later see that at least four specific molecular resonators must be postulated. In the first place, however, let us re-examine the facts which make necessary the assumption of the existence of one of these. This assumption is forced by the undoubted fact that the visual apparatus responds to electro-magnetic oscillations coming within a certain range of frequency, but does not respond to others—such as the ultra-violet, heat and Hertz waves—which in all respects save that of frequency (and wave-length) are entirely similar to light. It is certain at the outset that we must postulate the existence of at least one molecular resonator in the retinal rods and cones, for in no other way can we ac-
count physically for the selectiveness of visual response. If visual sensitivity depended at bottom upon non-resonating systems, the visible spectrum would be limited only by the varieties of electro-magnetic wave-length. As a matter of fact, the visible spectrum is the merest fragment of the physical spectrum. A complete physical spectrum capable of including all etheric waves known to us would be some twenty-two thousand miles in length; of such a spectrum only approximately thirty-four inches is correlated with visual experience, from wave-lengths 760$\mu m$ to 397$\mu m$.

The only hypothesis which has been propounded which can account for the selectivity of the retinal response without making use of the principle of resonance is that of G. Darzens, who supposes that the light is reflected from the pigment epithelium in such a way as to produce standing waves—the result of the interference of the incident and the reflected ray—within the cone and rod segments. Unfortunately the epithelium does not possess the requisite power of reflection; the incident ray must always be many times more intense than the reflected ray. Darzen supposes that the lengths of the standing waves produced determine the nature of the response. Even if we could believe in the actuality of such waves in the case in point, it would be difficult to given an acceptable account of the mechanism by which they brought about specific stimulation.

In the case of normal vision, of at least two resonators
must postulate the existence of two molecular resonators. The reasoning is very simple. Psycho-physical experimentation shows that

the hue of the visual sensation which appears at any point in the visual field is, under standard conditions a constant function of the wave-length of the light which falls simultaneously upon a corresponding point of the retina. We may assume that the quality of the sensation is paralleled psycho-physically by a particular qualitative and quantitative modification of the visual cortex. This means, then, that the processes of the cortex are, under standard conditions of the organism and of the stimulus, representable as a function of the wave-length of the stimulating light. Now the fact that the hue of the sensation changes qualitatively as we alter the wave-length only quantitatively seems to show that there is also some underlying qualitative change in the physical excitabilities, and suggests the existence of at least four separate resonators in the end organ. But this suggestion is not capable of immediate verification. Even though we have found ourselves forced to admit that the divergent qualities of the sensations demand divergent excitations in the corresponding cortical neurons (cf. page 252), we may still adopt the viewpoint of Donders and others and hold that these excitations are determined by the quantitative changes occurring in a smaller number of retinal mechanisms. But we can easily show that this latter number cannot be less than two. The most superficial explanation that could be given of the functional relationship existing between the cerebral state, C, and the frequency of the stimulating light would be to say that since any resonating system will respond more or less to periodic forces with which it is not exactly in tune, and since the intensity of this response will be proportional (in some function) to the degree of approximation
of the stimulus frequency to the natural frequency of the resonator, we must suppose that with a single resonator the intensity of the nerve impulse would vary as a function of the wave-length and hence that the resulting cerebral state should vary in the same way. From the nature of our conception of a molecular resonator, we can write: \( \dot{m} = e f(\lambda) \), where \( \dot{m} \) is the rate of decomposition of the resonating substance, \( e \) is the intensity of the stimulating light and \( f(\ ) \) a function describing the manner in which \( \dot{m} \) varies with a changing frequency of stimulus. Since we must suppose the cortical process or state to depend upon the reaction--stimulation--going on at the retina, we may write: \( C = f[e f(\lambda)] \), and we may naively imagine that this is an adequate description of the manner of interdependency of sensation quality with wave-length, only a single resonator being postulated. But that it is not really an adequate description can easily be shown, for the form of the function is such that any determinate state of \( C \) which can be brought about by the selection of an appropriate value of \( \lambda \) can equally well be caused by the proper value of \( e \); in point of fact the hue of a sensation cannot be given any desired value and composition simply by changing the intensity of the stimulating light. The most obvious difficulty with the conception lies in the fact that the maximum of responsiveness for a single resonator underlying our experience of the entire visible spectrum must lie approximately in the middle of the latter, and that on either side of this maximum there would surely be values in intensity of response, which would be the same, and that consequently the hue distribution in the visible spectrum should be duplicated on either side of the middle point. As a matter of fact no such duplica-
tion is observable. But—as we have indicated—the conception of a single resonator as the basis of visual response also falls down on account of the fact that we do not find in experiment that in increasing the intensity of a light of constant wave-length from zero to a maximum, the corresponding sensation passes through the whole gamut of hues. If the cerebral state depended only upon the intensity of the response we ought to be able to induce this state in two ways, either by altering the frequency of the stimulus, the energy remaining constant, or by changing the energy with the frequency constant. As a matter of fact, only the first mode of variation is effective.

**Effect of Two Resonators on Functional Relation of Hue and wave-length.**

But if we postulate the existence of at least two molecular resonators tuned to different frequencies this difficulty disappears, upon the assumption of two distinct impulses sent to the cortex and corresponding in intensity with the degree of response of the two resonators. For in this case we can express the cortical processes as a function of the ratio between the concomitant states of excitation of the two responsive systems, and we have every reason to suppose that this ratio would remain relatively constant with intensity changes in light of constant wave-length, but would vary rapidly when the intensity was held constant but the wave-length altered. This may be put in mathematical form in the following way. Let us designate the two resonators as $m_x$ and $m_z$, and their relative concentrations (molecules per cubic centimeter) in the end organs as $m_x$ and $m_z$ respectively. Then we can express the two laws of their decomposition under the influence of light as $(dm_x/dt) = \dot{m}_x = e f_x(\lambda)$, and $(dm_z/dt) = \dot{m}_z = e f_z(\lambda)$, since—other things
being constant—the changes caused by a light ray are proportional to its intensity. Now we may represent the cortical process $C$ as a function of the ratio which exists between $\bar{m}_x$ and $\bar{m}_z$, thus: $C = f_C(\frac{\bar{m}_x}{\bar{m}_z}) = f_C \left[ \frac{e^{f_x(\lambda)}}{e^{f_z(\lambda)}} \right]$, or $C = f_C \left[ \frac{f_x(\lambda)}{f_z(\lambda)} \right]$

and since the nature of the functions $f_x$ and $f_z$ is not such as to necessitate any duplication of specific values of this ratio as $\lambda$ varies, there is no reason to suppose that there will be a duplication of cortical states for different values of $\lambda$. On the other hand the function $f_C$ may be of any conceivable variety, according to the nature of the cerebral mechanism.

If by the hue of any sensation, $H$, we mean the attributive composition of the quality of this sensation, $S$, with respect to the hues, $R, Y, G$, and $B$, we can write $H = f_H \left[ \frac{f_x(\lambda)}{f_z(\lambda)} \right]$ on the basis of the fundamental principle of psycho-physical parallelism (cf. page 113). But if this relation holds it is possible to assume that so far as the dependency of the hue of a sensation upon the wave-length of light is concerned, there is no necessity of postulating the existence in the retinal rod and cone segments of more than two specific molecular resonators. We have been able to demonstrate the necessity of a system of retinal resonators having at least two elements without any appeal whatsoever to such complex phenomena as those presented in "color mixture," which customarily serve as the basis of an argument of this sort.

Reasons for Postulating At Least Three Specific Molecular Resonators...

But by taking advantage of an elementary piece of knowledge with regard to the effect of a mixture of lights in stimulation, we may make further advances along the
same line. This piece of knowledge is the fact that there are certain combinations of lights which when thrown upon the same area of the retina induce a sensation of zero chroma (cf. page 93), which, in other words fail to induce hues at all, but induce white, black, or gray. In "color-mixture" experiments it is usually the custom to compare the sensations induced in adjacent parts of the visual field by two lights which are thrown upon adjacent parts of the retina. One of these lights is homogeneous (cf. page 152); the other is heterogeneous. The composition of the latter may generally be so adjusted that the two adjacent images in the visual field become alike in quality. They are then said to "match." Now let us attempt to determine in the first place upon what principles the possibility of inducing the same sensation quality with different stimuli must be supposed to depend. Two lights $L_{ht}$ and $L_{hm}$ (heterogeneous and homogeneous, respectively) are thrown upon adjoining areas of the same retina. $L_{ht}$ has a composition $L_{ht} = L_{e_1 \lambda_1} + L_{e_2 \lambda_2}$, while $L_{hm} = L_{e_a \lambda_b}$ (the subscripts $a$ and $b$ being arbitrary). Now the two molecular resonators, $M_x$ and $M_z$, which we have been forced to postulate, respond in accordance with the laws: $\dot{m}_x = e f_x(\lambda)$ and $\dot{m}_z = e f_z(\lambda)$. The hue of the sensation is determined by $H = f_h \left[ \frac{f_x(\lambda)}{f_z(\lambda)} \right]$. In the case to be studied there are two sensations, which we may designate as $S_{hm}$ and $S_{ht}$, corresponding with the two stimuli, as indicated by the subscripts. We have also to consider the hues of these two sensations, $H_{hm}$ and $H_{ht}$. Now $H_{ht}$ is induced by the action of light having two different frequencies, and the rate of decomposition of the two resonators, $M_x$ and $M_z$ in the area of the retina thus doubly stimulated will
be the sum of the rates which would attend stimulation by each of the component lights when given singly, so that \( \dot{m}_x = e_1 f_x(\lambda_1) + e_2 f_x(\lambda_2) \), and \( \dot{m}_z = e_1 f_z(\lambda_1) + e_2 f_z(\lambda_2) \), and the resulting sensory hue will be determined by:

\[
H_{nt} = f_h \left[ \frac{e_1 f_x(\lambda_1) + e_2 f_x(\lambda_2)}{e_1 f_z(\lambda_1) + e_2 f_z(\lambda_2)} \right]
\]

Upon the consummation of a match between \( S_{nt} \) and \( S_{hm} \) we have:

\[
H_{hm} = H_{nt} = f_h \left[ \frac{e_1 f_x(\lambda_1) + e_2 f_x(\lambda_2)}{e_1 f_z(\lambda_1) + e_2 f_z(\lambda_2)} \right] = f_h \left[ \frac{f_x(\lambda_b)}{f_z(\lambda_b)} \right]
\]

It will be seen that whereas in the case of the homogeneous light the energy of the rays does not affect the hue, in the case of the heterogeneous light \( \lambda_1 \) and \( \lambda_2 \) may be held constant while \( e_1 \) and \( e_2 \) are varied, and the result will be a variation of \( H_{nt} \). This is the principle upon which the typical determination of a "color-system" is carried out (cf. page 412).

Now it is found experimentally that when \( e_1, \lambda_1 \) and \( e_2, \lambda_2 \) are properly chosen the chroma, \( h \), of \( S \) (cf. page 93) may be reduced to zero, a corresponding increase in tint occurring. The lights thus chosen may be described as complementary lights, and the sensory hues (composition of the quality of \( S \) in terms of R, G, Y, and B) corresponding with these lights—when employed separately—may be called complementary sensory hues. Let us inquire concerning the conditions underlying this complementation. We have already seen—in our attributive analysis of the elementary visual sensation (page 94)—that the two derived sensory attributes of tint and chroma are correlated in such a way that \( t = \text{const.} \).
dependent upon the purity of the light employed. When only
two homogeneous lights are mixed, within certain limits the
tint of the induced sensation varies in the same sense as the
difference between the wave-lengths of these lights, the chroma
varying inversely. Now we have supposed that the hue of a sensa-
tion may be determined by two functional relations containing
the wave-length of the stimulating light, \( f_x(\lambda) \) and \( f_z(\lambda) \). It
appears that this supposition is justified so far as reference
is had only to approximate determination. But we are also led
by experiment to the conclusion that the amount of hue or the
chroma of any sensation is determined, in case heterogeneous
light stimuli are employed, by some other function of the two
wave-lengths involved, so that \( h = f_k(\lambda_1, \lambda_2) = \text{const.} - t \).
We explain the dependency of \( H \) upon \( \lambda \) by the postulation of two
types of molecular resonators tuned to different frequencies.
By the use of what hypothesis shall we explain the function:
\[
h = f_k(\lambda_1, \lambda_2)\]
In the first place, it seems advis-
able to say something concerning the nature of the above func-
tion. It is found that if \( \lambda_1 \) has a value of about 750 (cf. page
151) and \( \lambda_2 \) is decreased from 750 indefinitely, the energy of
the two lights being kept as nearly as possible constant, the
chroma of the resulting sensation decreases until it becomes
zero, and then increases once more. At the point at which the
chroma is zero the tint of the sensation is a maximum. Now we
attribute the constitution of the hue of a sensation to the ra-
tio between the values of \( \dot{m}_x \) and \( \dot{m}_z \) but it is evident that we
cannot attribute the amount of hue, or chroma, to this variable,
for the hue may have the same constitution whether the stimulat-
ing light is heterogeneous or homogeneous, whereas the chroma may be entirely different. Now we have seen that the chroma of $S$ seems to depend upon differences in wave-length among the constituents of a heterogeneous light which is acting as a stimulus, and that with certain lights, as this difference is increased $h$ falls to zero and then rises once more. Since we have no reason for supposing that the rate of decomposition of the molecular resonators is affected by the simple presence of light frequencies possessing a certain difference in amplitude we must conceive the decrease in chroma to be due to some reaction occurring between the end products of this decomposition which prevents the production of a normal visual impulse. If we mix lights of approximately $\lambda = 500$ and $\lambda^\prime = 700$ at the proper intensities a sensation will be induced which is of the same hue as that induced by a light of $\lambda = 700$, but which has a very much reduced chroma. Now if the hues are the same we must be able to write:

$$H_{ht} = H_{hm} = f_h \frac{e_1 f_x(500) + e_2 f_x(700)}{e_1 f_z(500) + e_2 f_z(700)} = f_h \frac{f_x(700)}{f_z(700)}$$

This equation means that in each case the ratio between $\hat{m}_x$ and $\hat{m}_z$ is the same. In what way shall we explain the fact that in one case the resulting sensation quality is so different from that in the other. We cannot explain it by assuming that it is dependent upon some new function of $\hat{m}_x$ and $\hat{m}_z$ because in that event we should be able to fulfil the requirements of this function by means other than varying $\lambda_1$ and $\lambda_2$. It is obvious, therefore, that it is necessary to postulate the existence of at least a third molecular resonator. This resonator may be sup-
posed to be governed by a law $\dot{m}_y = e f_y(\lambda)$, which yields a maximum at a point different from that of either $M_x$ or $M_z$. Hue may then be determined by a function $H = f_h(\dot{m}_x/\dot{m}_z)$, as before, while chroma may be determined by some function $h = f_t(\dot{m}_x, \dot{m}_y)$ or $h = f_q(\dot{m}_y, \dot{m}_z)$. It appears, then, that by the application of a method of reasoning which involves absolutely no assumptions beyond those necessitated by our conception of a resonator, and of the causal relation we have been able to prove that in order to account for the crudest psycho-physical relations of visual sensation at least three separately acting resonators must be postulated. The proof of the existence of at least two resonators is based upon the fact that within fairly wide limits our ability to discriminate between lights of different wavelengths is independent of stimulus intensity. The proof of the existence of at least three molecular resonators is founded on the fact that within certain limits we are able to discriminate differences in wave-length in heterogeneous light and that the mechanism for this discrimination is independent of that which determines the hue of a sensation. This proof is quite different from one based upon conceptions of primary colors.
Chapter 13: Some Necessary Physical and Chemical Properties of the Molecular Resonators.

In assuming that the response of the retina to light depends upon the presence in the rods and cones of specific molecular resonators which are broken up under the action of light into positive and negative ions, we have admitted that the phenomena of visual response cannot be governed by principles any less complex than those underlying chemical processes. In attempting to develop a complete hypothesis of visual sensitivity upon the basis of this conception of molecular resonance and consequent decomposition, we must of necessity take into consideration all of the recognized general attributes and modes of activity of chemical substances. These are fairly definite, but they are not especially simple in character. Every hypothesis of visual response which makes use of chemical postulates must inevitably face the danger of encountering harsh criticism on account of its complexity, -- the number of terms and constants and variables which must necessarily appear in any complete account which is given of it. In spite of this manifoldness, however, the chemical view-point will prove none too rich in suggestions for one who desires to make a system--even a complicated system--out of the multitudinous and difficultly understandable facts of visual sensitivity.

We have seen in a foregoing chapter that it is absolutely necessary to postulate the existence in the retinal rods and cones of at least three
specific molecular resonators. Let us clearly understand what the word specific denotes in this context. It obviously means, in the first place, resonance to particular and peculiar light frequencies; no advantage would arise from the presence in the retina of three mechanisms responding to the same sort of light; one of the resonators must be specially sensitive to short wavelengths, another to longer wavelengths, etc. But this specificity in resonance must depend upon specificity in structure; each of these three molecules is built differently from the others. Hence it is probable that the end products resulting from decomposition of these molecules under the influence of light will be characteristic, and not identical in each case. There are certain chemical constants—shortly to be discussed—which characterize every chemical species; for each of the three—or perhaps more—molecular resonators that must be postulated these constants will possess typical and peculiar values. In assuming a pluralistic chemical basis for visual response we have assumed that it will be necessary to take into consideration a number of groups of individualized properties, which will have to be dealt with in any attempt to work out the details of the visual process. Some of these properties we shall now consider.

The Concentration of the Resonators...... Perhaps the most important conception which must be applied to each specific molecular resonator is that of specific concentration. Any individual resonator is a single molecule, but when we speak of molecular resonators in a general way we imply the presence of a large number of molecules, all of a kind, which react with the light in the way characteristic of their species.
At any time, in any particular rod or cone cell, or in any particular region of any particular rod or cone cell, each one of these molecular species will be present in definite concentration; there will be a certain number of representatives of the species in the cell or in the region. We shall express this concentration in terms of molecules per retinal element, and if \( M_n \) is the symbol for the specific resonator under consideration we shall employ the symbol \( m_n \) to mean its concentration in any region which we may happen to be investigating. The concentration of one species has no logical connection with that of any other species.

When chemical change occurs molecules of one sort are destroyed while others are being built up. This involves a change in the concentration of each. The number of molecules of any species produced per second in a cubic centimeter of volume may be defined as the rate of change of the concentration of this species in that volume, provided the only change occurring is a chemical one. This quantity may be written as \( \frac{dm_n}{dt} = \dot{m}_n \), where the molecular species concerned is that described by the symbol \( M_n \). This conception of rate of change of concentration is generalized in such a way that it comes to mean not the real rate of change in any region, but, instead, that which would be real if the only process going on there were the one under immediate consideration. Thus, when the apparent rate of change of the concentration of \( M_n \) in a certain region is zero, we may still look deeper into the processes of that region and find that there exists a simultaneous and equal composition and decomposition of \( M_n \), in which case we can speak of two rates of change of concentration, \( \dot{m}_n' \) and \( \dot{m}_n'' \) such
that \( \dot{m}_n' = -(-\dot{m}_n') \). The rate of change of concentration of one chemical substance in a region may not have anything to do with the rates of change of concentration of other substances not involved in the same reaction with them. We usually speak of a generalized rate of change of this sort as a reaction velocity; it may be positive or negative according as it tends to increase or decrease the concentration of the specific substance under discussion.

In the case of light-sensitive substances the reaction velocity is either increased or diminished by the incidence of light. Assuming—in the case of our molecular resonators—that the light involved is of such a frequency as to produce a maximum effect, if we increase the intensity of the light there will be a corresponding increase or decrease in the velocity of the reaction. If the increase in light intensity is \( \Delta e \) and the increase in reaction velocity is \( \Delta \dot{m} \), the ratio \( \Delta \dot{m}/\Delta e \) is a constant characteristic of the substance \( \dot{m} \); we may call this its light sensitivity. Each molecular resonator which we postulate we must regard as the possessor of a specific light-sensitivity. In general we shall symbolize this quantity by \( q_n \), where \( n \) is the subscript describing a particular molecular resonator.

The conception of resonance applied to a chemical substance decomposing under the influence of light, necessitates a rate of change of the reaction velocity with respect to the frequency or wave-length of the light. If we consider a light ray of constant intensity the wave-length
of which is subjected to alteration, to be acting upon a certain resonant light-sensitive substance, the reaction velocity of this substance, \( \dot{m}_n \), will exhibit an increase (or decrease) \( \Delta \dot{m}_n \) for every variation of the wave-length through \( \Delta \lambda \). Thus we may define a quantity \( \beta_n = \Delta \dot{m}_n / \Delta \lambda \), which we may call the resonance gradient of the substance \( m_n \). This quantity is obviously not a constant, for the reason that the function \( \dot{m}_n = f_n(\lambda) \) possesses a maximum at which the resonance gradient must be zero, and since when \( \lambda \) deviates extensively from this maximum value (of \( \dot{m}_n \)) the resonance becomes very slight. Let us call functions of the general type \( f_n(\lambda) \), resonance functions. It is obvious that the resonance gradient at any value of \( \lambda \) is the value of the first derivative of the resonance function for that wave-length. The nature of functions of this sort is illustrated in the accompanying graph. In the graphical representation of the resonance functions of the special molecular resonators which we shall be forced to describe in the course of this thesis the abscissae employed will be wave-lengths of light, while the ordinates will express the number of molecules broken up per retinal element per second per unit light intensity. Several of these curves—for several specific resonators—may be drawn with respect to the same axes. Then if we multiply the ordinates of each of the curves for any particular wave-length by the intensity of the light possessing that wave-length we shall determine the reaction velocity of each of the molecular resonators represented, under the influence of light of the specified frequency and intensity.

The fact that a chemical reaction velocity is always

a rate of change of concentration of the reacting substance
The Law of Chemical Mass Action and Reversibility of Reactions

has certain interesting consequences. Among these is the fact that although it is true that the rate of decomposition of a light sensitive substance under the influence of light is proportional to the intensity of the light, other things being equal, the apparent rate of change of the concentration will not be thus proportional, on account of the alteration of the initial concentration of the reacting substance which takes place so that at every instant the reacting mass is different from what it was at the preceding instant. The law of chemical mass action states that the rate of any chemical reaction is proportional to the concentrations of the reacting substances and to certain constants. The origin of this law is self-evident; the constant which appears in any case represents the inherent capacities of the molecules concerned for disintegration or combination; if we select \( n \) molecules of this sort, \( kn \) will disintegrate or react in unit time; if however we take \( 5n \), we shall expect \( 5kn \) to react in that time; hence, if in each case the molecules are all contained within the same volume, we write that the rate of change of concentration of these molecules which obtains at any instant is proportional to the number of molecules present in unit volume at that instant, \( m = kn \). This is the case with what is called a mono-molecular reaction. When more than one species of molecule is concerned in the reaction, the rate of change is proportional to the concentrations of each of the species, thus: \( \dot{m} = knn' \) where in each case \( k \) is any constant. But there is another important consideration which enters into the discussion of the rate of chemical reactions, and this is the conception of reversibility of reaction. If a certain molecule \( M_n \)
reacts according to the equation: $M_n \rightarrow I_+ + I_-$, the end products $I_+$ and $I_-$ will also react according to the equation: $I_+ + I_- \rightarrow M_n$. Each of these reactions will possess a characteristic constant which shows how the reaction velocity is related with the concentration of the reaction substances at any instant. Now it is obvious that the apparent rate of change of concentration of $M_n$, for example, will be equal to the difference between the rates at which the constructive and the destructive reactions figured above proceed. The apparent reaction velocity will depend upon the nature of two actual reaction velocities; a state of chemical equilibrium is merely one in which the forward and reverse reaction possess equal speed. Now if we suppose light to accelerate the analytic reaction and to have no effect upon the synthetic one, an increase in the intensity of the light may or may not be accompanied by a proportional increase in the apparent reaction velocity, according to the nature of the reverse reaction. We shall have more to say concerning this point when discussing the hypothetical basis of Fechner’s logarithmic law in the department of visual sensitivity. Suffice it here to note that since every chemical change is—theoretically at least—reversible in character, we must be prepared to take into consideration at least two different reaction constants—describing the proportionality existing between the concentration of reacting substances and the velocity of the reaction—in our discussion of the behavior of the molecular resonators under the influence of light.

Light as a Catalyzer. It is very improbable that the molecular resonators—the existence of which in the cone and rod segments we have postulated—can safely be regarded as
undergoing decomposition only under the influence of light. Indeed to regard them in this way would be to contradict the fundamental principle of chemical action. \( M_n \) - we must decide -- is continually breaking down even in the absence of light. The end products of this decomposition accumulate until the reverse reaction becomes equal in speed to the reaction of decomposition; the result is a state of kinetic chemical equilibrium between \( M_n \) and its decomposition products \( I_+ \) and \( I_- \). This automatic disintegration of \( M_n \) may be attributed to the effect of the impacts of the molecules in the heat vibrations of the substance; the opposing synthesis is due to the normal chemical affinities acting in the event of favorable collision between \( I_+ \) and \( I_- \). Now since the disintegration products of \( M_n \) are ions this state of equilibrium is merely one of normal ionization of the substance; in the equilibrium state \( M_n \) will be partly ionized, partly unionized. The percent ionization will obviously depend upon the relationship which exists between the reaction constants of the analytic and synthetic reactions respectively, being determined by an equality (with opposite signs) of the two reaction velocities. The effect of the introduction of a light ray into this chemical system is merely to increase the constant of the disintegrative or ionizing reaction, that is, virtually, to increase the ionization. The resonance effect is added to that due to the heat impacts alone. Light, then, acts in a manner somewhat similar to that characteristic of a catalyzer; it does not initiate the chemical reaction, but simply aids it. Light differs from a catalyzer in being able to alter the position of the equilibrium point; this is a very important difference. It is important, also,
to bear in mind the fact that each molecular resonator which we postulate must be conceived of as possessing a definite unstimulated ionization, which we shall call its normal ionization. This is a percentage measure characteristic of the substance, and must not be confounded with the light sensitivity (cf. page 213), which is the character involved in any modification of this normal ionization under the influence of light. It is conceivable that a particular resonator should possess a high normal ionization, combined with a low light sensitivity; in fact this combination seems the most likely of any.

The Initial Production of the Resonators..... In our discussion of the mechanism of the visual impulse we shall find it necessary to assume that the end products of the ionizing reaction occurring in the molecular resonators are used up in the production of the afferent nerve current and other phenomena of the visual response. This being the case the disintegrative reaction will permanently predominate over the integrative one, and the result will be a depletion of the rods and cones of the light-sensitive substances. In order that visual stimulability should be maintained it is necessary to assume that a mechanism exists whereby new resonating molecules are built up from the cell lymph. This mechanism is undoubtedly enzymic in nature, and we have already been led to postulate the presence of specific aesthesogenases engineering specific chemical reactions which reduplicate the several molecular resonators (cf. page 193). These initial reactions which give rise to the resonators in the first place must be regarded as possessing characteristic constants. Each aesthesogenase finds its own proper substrates
in the lymph. These may be the same or different for different aesthesogenases. In any event each aesthesogenetic reaction must be regarded as determined by at least two definite reaction constants, describing the relation existing between the synthetic and analytic reaction velocities and the concentrations of the reacting substances. We shall speak of these aesthesogenetic reactions as if they were syntheses; this is probable but by no means certain. If they are indeed syntheses they cannot, of course, be identical with the reversed ionization reaction characteristic of the resonators alone; the relationship between the two reactions must be something of the following sort:

\[
\text{(Aesthesogenetic React.) (Resonance Reaction..)} \\
\text{ABE + C} \rightleftharpoons \text{ABC} \quad (= \text{M}_n) \rightleftharpoons \text{A} + \text{BC} \quad (= I_+ + I_-)
\]

The second reaction is that influenced by the light. Equilibrium in this system must evidently depend upon a state of balancement of at least four different reaction velocities. The concentration of M\(_n\) and hence the velocity of the resonance reaction—whether or not assisted by light—may obviously be affected by changes in the concentration of A\(\bar{B}\) and C—the aesthesogens—(cf. page 193) or in the activity of the aesthesogenases. We shall make use of these conceptions in explaining the phenomena of visual fatigue and adaptation. It is apparent that the removal of the compounds A and BC (= I\(_+\) and I\(_-\)) in the production of the visual impulse (cf. page 237) will result in a movement of the double reaction towards the right; this is the mechanism of supply of the resonating molecules. Whether or not the aesthesogenetic reaction is actually synthetic makes no particular difference in our discussion; the underlying chemical principles
will be the same. It is probable that the substances $\overline{AB}$ and $\overline{U}$ are specially prepared in the cells of the pigmented epithelium (cf. page 163), and from this tissue penetrate the rods and cones where the aesthesogenetic reaction takes place; this reaction could not be permitted to take place elsewhere without forfeiture of those prerequisites of clear visual stimulation which we have already discussed in Section XVIII. The aesthesogens are specific for each resonators; $\overline{AB}$ and $\overline{U}$ in our equations are $\overline{AB}_n$ and $\overline{U}_n$.

The Color of the Molecular Resonators. The only physical characteristic of the molecular resonators which deserves mention is that of color. A substance which breaks down chemically under the influence of lights of specific wave-length in accordance with the principle of resonance which we have set forth will of necessity absorb light of these wave-lengths more strongly than that possessing other wave-lengths. Other things being equal, a specific resonator should present a physical color more or less complementary to that which it mediates in sensation. The resonator responding to lights having a wave-length about 500 $\mu\mu$ might be expected to transmit or reflect lights corresponding with the ends of the visible spectrum and thus to appear scarlet or purplish red in color. Other things may not be equal, however; it is not certain that all of the light energy absorbed by the substance will go into chemical change. Selective light absorption may always demand resonance, but resonance does not inevitably result in chemical change; it may result in fluorescence, the energy being radiated again with a lower frequency.


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PART SEVEN: THE NATURE OF THE VISUAL IMPULSE.

Section XX : Is the Visual Impulse a Specific Energy?

The Visual Impulse in Current Hypotheses

Next in importance to the problem of the nature of visual stimulation is that of the character of the visual impulse which is its immediate result. Strange to say this problem has received scant attention at the hands of modern theorists in the field of visual sensitivity. Possibly this state of affairs may be explained by the fact that the existing situation in visual theory is such that any consistent attempt to propound an hypothesis of the visual impulse would inevitably result in a conflict between its author and a very popular and useful doctrine, that of specific nerve energy. The original theory of Thomas Young was proposed before Johannes Müller's time, and yet, although it antedated the definite statement of the principle of specific energies by a quarter of a century, it was very admirably adapted to that principle, and in the hands of Helmholtz, as we have seen, the three-color hypothesis became a three-fibre hypothesis. It was not long however before experimental results forced the conclusion that three fibres were not truly requisite in the production of even the typical visual response. The result, however, was not a modification of the three-component hypothesis to fit the demands of a single and simply quantitatively variable nerve impulse, but was, instead a neglect of the whole problem; but implicitly the theory of specific nerve energy as applied to the separate fibres of the optic nerve was already refuted.

If we examine current

hypotheses in the hope of finding some definite statements with regard to the nature and mechanism of the visual impulse we are disappointed. But it is apparent that in all of these hypotheses the doctrine of specific nerve energy has not been rigidly regarded. The pragmatic attitude and physical bias of the modern upholders of the Young-Helmholtz hypothesis precludes any definite statement from them concerning the manner in which the three fundamental retinal excitations come into relation with cortical processes and with sensation. Hering, in his turn, refuses to state whether the three hypothetical visual substances which he postulates are retinal or central and thus easily escapes the difficulty of describing the connection existing between the retina and the centers. Other theorists, such as Mrs. Ladd-Franklin, simply affirm that the nerve is excited by certain retinal processes and that certain sensations result; a non-specific energy is implied, but its mechanism is not described. Edridge-Green, in his hypothesis, supposes that identical retinal cones may be differently stimulated by the decomposition in their vicinity of different forms of visual purple and that special "colour-perceiving centers" which exist in the brain are capable of sorting out the central effects of this differential stimulation. The stimulation is regarded as electrical in nature, but how its results can in particular cases give the brain any basis for "colour-perception" is left unsaid.

Definition and Basis of the Specific Energy Theory........... Helmholtz defines the principle of specific energy in the following

1 EDRIDGE-GREEN, F. W.: The Hunterian Lectures (1911); Lond., (1911); p. 10.
way: "By the excitation of any sensory nerve-fibre whatsoever, one can only produce sensations which possess the modality of a single and a constant determinate sense, and any excitant whatsoever, however little it acts upon that fibre can never provoke other sensations than those possessing the modality peculiar to that sense." Now the experimental work of Hering, Isaachsen and Holmgren has made it clear that all of the attributes of the elementary visual sensation may be induced by the application of appropriate light stimuli to a single foveal cone. We have seen in a preceding section of this thesis that it is impossible to account for the manner in which the attributes of the luminous stimulus are correlated with those of the elementary sensation without assuming the presence in the retinal cones of at least three independent molecular resonators, each of which possessed an independent causal connection with the processes of the cortex and thence with those of the visual field. The exact mechanism of that causal connection we have not yet specified, but further examination will show that either a "three-fibre" or a three-quality visual impulse must be postulated. Histological evidence makes it certain that single retinal end-cells are not connected with a plurality of nerve-fibres; on the contrary, in the majority of cases several end-cells are connected with a single fibre; there are seven million cones and one hundred and thirty million rods in the human retina, but there are only half a million fibres in the optic nerve. If strictly applied the definition of specific nerve

1 HELMHOLTZ, H.: Optique Physiologique; Paris (1867); p. 263.
3 J. Q., p. 237.
energies given by Helmholtz would necessitate the postulation of six distinct "fibres" in the optic nerve for each cone cell, since there are at least six distinct qualities of visual sensation which can be induced by excitation of a single cone. If the nature of the sensations which follow upon stimulation of a single nerve ending by the use of stimuli of various intensities can differ only in degree, never in quality, then we cannot admit that a single optic nerve fibre is capable of being so excited as to induce the vast variety of qualities which may be observed in the elementary sensation.

The doctrine of specific nerve energy is based upon the conception of the constancy of functioning of a constant or identical structure. Sensation is regarded as the central process of a structure whose state of excitation depends upon that of the nerve fibre with which it is continuous. If the nerve impulse is determined in its character by the structure of the fibre and is due to the simple arousal of a characteristic potentiality by disturbing outside forces, then these forces can produce different effects upon the fibre only by producing different quantitative effects, and the resulting central process can differ only quantitatively, i.e., all of the processes induced will be capable of description mathematically in terms of the same units. Since the principle of specific energy appears to hold not only for nervous tissue but for all of the cells of the organism, each--upon stimulation--responding with its own characteristic function, no matter what the nature of the stimulus, it seems reasonable to suppose that the fundamental assumption of Müller is correct; a typewriter constructed to write in English print will never yield a page in Chinese, even with a Celestial at the keyboard. The stimulus does not produce the nerve
impulse; it merely releases it. But admitting that the response of a nerve fibre to a stimulus is always of the same general character, is not equivalent to an admission that the central effects of different stimuli applied to the same fibre may not be supposed to differ widely in character. The swallowing movements of the muscles of the throat and esophagus are essentially constant in character no matter what the stimulus; the effects upon the digestive system may be extremely diverse. In the case of the nerve impulse some part of the stimulus itself, or of one of its immediate products in the end organ, may be carried along with the nerve impulse. On the other hand, it is quite possible that simple differences in the intensity of the afferent nerve current may result in such a shifting of central connections that very wide qualitative differences will be observable in the central effects. A mechanism of neural relays may readily be imagined which would result in an entire change of the cortical connections when a certain critical degree of intensity had been reached. A gradual, balanced, shifting of central excitabilities is also easily pictured. There can be no doubt that the cortical mechanism is very complex and also quite definite in its reactions. Too little attention has been paid by physiologists to the problem of imagining definite conductive and resistive neural systems capable of being regarded as the hypothetical basis of the reflex, the instinctive, and even the higher "conscious" reactions of the organism.

The Cone Fibre Impulse is not a Specific Energy.................

It will be perceived that the conception of the specificity of a nerve energy is relative in nature. The energy of a particular nerve fibre bundle in the optic nerve
may fail in specificity, while that of individual fibres is perfectly specific. Further more, it conceivable that the energy of an individual fibre should be non-specific while that of some component of the fibre remains specific. Now we know that the majority of nerve fibres contain within their mass continuous smaller strands called fibrils. It has been suggested that these fibrils are the actual conductors of the nerve impulse. Since there are usually many fibrils in a single fibre, we may—if this suggestion should prove tenable—hold that the conductions taking place along different fibrils of the same fibre are qualitatively distinct, but in themselves are capable only of quantitative variation. Now if we accept as valid Von Kries' view that the retinal cones only, mediate sensations possessing the attribute of hue there is a certain peculiarity of structure exhibited by the cone-cells which acquires special significance. This is the relative thickness, the heavily fibrillated character and the complex connections of the cone cell fibre as compared with the rod cell fibre. It will be remembered (cf. page 158) that while the rod cell fibre ends in a "knob", the cone cell fibre terminates in a "foot". This latter structure is of such a character as to permit the separate connection of the fibrils of the cone cell fibre with those of the dendrite of the bipolar cell of the outer nuclear layer of the retina with which it is in contact. If the neuro-fibrils are actually specific conductors we should expect to find them specifically connected in the cone cells but not necessarily so in the rod cells. There can exist hardly the slightest doubt that the visual impulse

as it is carried by the cone fibres and their connections is not a specific energy. We have proven in Chapter 12 (pages 199-210) that at least three independent mechanisms of stimulation must exist in each retinal element which is capable of mediating the simplest of the psycho-physical relations of the elementary visual sensation. The same argument also proves the necessity of postulating the existence of three independent means of transmitting the effects of the activity of these three independent stimulation mechanisms to the cortex, or else the presence of a qualitative modification of the impulse in three different directions or dimensions (cf. page 76).
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Section XXI : A Definite Hypothesis of the Visual Impulse.

The Retinal and Cortical Changes in Visual Stimulation..................

We have thus far in our discussion reached the conclusion that there exist in the unstimulated rods and cones certain ionized substances which we have called molecular resonators. When light falls upon the retina the effect is an increase in the ionization of these substances provided the wave-length of the light in question is such as to produce resonance in the unionized molecules. Now we know that the incidence of light at the retina is the occasion of a change in the sensations present in the visual field. Since we believe that the elementary sensation is directly correlated only with a cortical process, it is necessary to assume that this change in ionization which occurs in the retina brings about some change in the cortex by way either of the initiation of or a change in the visual impulse.

The Elements of the Elementary Visual Response.

Let us consider the case of an elementary visual response, V.

This may be defined with reference to the elementary visual sensation, S. This latter, we remember, is defined as the sensation which exists at a point in the field of vision. Now we may consider such a sensation to be immediately paralleled by the activity of a group of cortical neurones, in the simplest case, by a single cortical neuron. The elementary cerebrosis thus defined is C, and must always be thought of as corresponding with a specific elementary sensation S (cf. page 62). The elementary visual impulse, I, which is responsible for the pro-
duction of C, may be regarded in the simplest case as a nerve current passing along a single nerve fibre of the optic nerve and tract, while the elementary stimulation, X, making up a part of the same elementary visual response, V, may be conceived as the response of a single rod or cone segment—typically the latter. We shall also speak of an elementary light ray, L, which is that ray having a cross-section equal to and coincident with that of the particular rod or cone segment which we are considering.

Now our conception of V as a causal sequence (cf. page 59) gives us the relations: \( X = f(L) \), \( I = f(X) \), \( C = f(I) \), and \( S = f(C) \). From this, if \( V \) is complete, we have \( S = f(X) \), where \( f \) in each case represents any state of interdependency.

This last relation, however, holds only by virtue of the possibility of writing the intermediate functions, and it is to the nature of the mechanism underlying one of these, viz., \( I = f(X) \), that we now turn our attention, always keeping in mind the conception of an elementary visual response.

Visual Stimulation May Exist Without Stimulus

Since the visual impulse and stimulation process are in all probability facts which can be quantitatively determined, let us write (cf. page 80): \( i = f(x) \), leaving to one side the question as to whether a single function of this sort will suffice to represent quantitatively the complete state of interdependency of impulse and stimulation. If the function \( i = f(x) \) is—as seems likely—continuous, we must assume that whatever the process is which is finally to be meant by \( i \), it must exist in some degree whenever \( x \) has any value (except some critical value) at all. Now it is evident that since so far as our hypothetical
studies have yet led us x must be considered as representing
the ionization of the molecular resonators, there must be certain
values of i corresponding to the normal ionization of these re-
sonators. (cf. page 217). To assume that this is the case in-
volves no inconsistencies at the present stage of our argument,
since it does not follow that the function, \( C = f(I) \), is con-
tinuous, or if we should conclude that this latter function is
indeed continuous we may still fall back upon the fact that
even without stimulation of the retina the visual field still
exists, i.e., there is sensation. We come then to a conclusion
which, if we interpret its description in accordance with the
common usage of the words, is paradoxical: visual stimulation
may exist without visual stimulus. This simply means, of course,
that the same process which follows the stimulus in the typical
visual response, may exist in a certain degree without the pre-
cedence of the stimulus.

The Specific Dependency
of the Impulse........ Now since the effect of light
upon the retina is the production
of an increased concentration of ions, positive and negative,
let us assume that the visual impulse is dependent in its in-
tensity upon the concentration of ions in the cones or rods, and
let us suppose, moreover, that it is dependent only upon the
concentration of one variety of ion, viz., the positive. If
\( i_+ \) and \( i_- \) represent the concentration of the ions \( I_+ \) and \( I_- \)
in the single cone segment which we are considering, and i is
the intensity of the elementary visual impulse originating in this
cone, we may write: \( i = f(i_+) \).

Let us now attempt to develop some definite hypothe-
sis of the visual impulse itself. The fact that the nerve impulse in general is accompanied by a moving wave of electrical negativity suggests that the impulse consists in an actual movement of ions along the fibre. If the negative wave which is observed in physiological experimentation to travel along the sheath of a stimulated nerve is not balanced by a simultaneous positive wave travelling in the core, we are inevitably forced to the conclusion that there is an actual movement of electricity along the nerve. But electricity is an atomic substance, and, so far as we know, its propagation in liquid or semi-liquid bodies is exclusively a matter of the movement of chemical ions.

The Nerve Impulse Consists In An Actual Propagation of Ions ..............

It may therefore be suggested that the visual impulse depends upon the state of ionization of the molecular resonators in the rod and cone cells by virtue of the fact that the impulse itself consists in a simple removal of either the positive or the negative ions along the nerve.

The Mechanism of the Nerve Impulse....... In spite of the fact that apparent charge which travels along the nerve is negative, we shall assume that the propagated ion is the positive one. This assumption results from an attempt to imagine in what way the visual ion may be carried along. We shall assume that the neuro-fibrils which characterize all nerve fibres, and which consist in very delicate threads running continuously within the dendrons and axis cylinders are the actual paths of conduction of the ions. These neuro-fibrils are to be thought of as molecular tubes, specialized structures within which it is possible for even single ions to travel without encountering great
resistance. This is a return to the theory of Descartes with reference to the mechanism of the motor nerves. The manner in which an individual ion or a group of ions may be imagined to be propagated along one of these molecular tubes will be described as follows. The non-fibrillar portion of the nerve fibre is made up of a mixture of substances certain of which are ionized, and others of which are capable of constituting an osmotic membrane which normally is equally permeable to the positive and to the negative ions. However, when a positive ion comes into contact with one of the neurofibrils the surrounding neural substance acquires a slight differential permeability, so that the negative ions are capable of moving within it more readily than the positive ions. This being the case the loss of negative ions into the surrounding tissues—say into the myelin sheath when this is present—results in the development of a positive charge within the core itself. The original positive ion thus finds itself placed within the influence of a positive electrical field. Since this is a state of disequilibrium, if the ion is free to move—and if, as will be the case, its charge is much smaller than that produced in the nerve—it will travel in one direction or the other along the neuro-fibril. If we suppose the ion to have had an original impetus in the afferent direction, it will move in this sense. The resulting process is obvious. As soon as the ion has moved into a new region of the nerve fibre the permeability of the neural substances about it for negative ions will be altered as before, a new state of disequilibrium will be produced and the process will be repeated, the ion moving continuously in one direction within the fibril.
The Origin and Special Mechanism of the Visual Impulse.............

Upon this hypothesis the mechanism involved in the origin of the visual impulse may be described as follows. The original ions involved are those due to the electrolytic dissociation of the molecular resonators present in the rods and cones of the retina. Now we must suppose the neuro-fibrils of the rod and cone fibres to terminate within the molecular field occupied by these ionized resonators. The fibrils have a diameter of about $2 \times 10^{-5}$ cms, which is approximately one thousand times the diameter of a hydrogen molecule. Presumably the ions with which we are concerned in the study of visual response are organic in their nature, and may be supposed to have a diameter as great as $2 \times 10^{-7}$ cms., or some ten times that of the hydrogen atom. For such an ion the end of the neuro-fibril --which we will call a neural transmitter--would present a width one hundred times its own diameter. From this, of course, it does not follow that the molecular tubes, the existence of which we have postulated, are coincident in size with the whole neuro-fibril. At any rate it seems unnecessary to suppose that single ion only are picked up at a time by the fibril terminus, the neural transmitter; undoubtedly the ions enter in crowds. Now the effect of an excitation of the electrolytic peristalsis which we have supposed to be set up in a neuro-fibril and its surrounding neural substance by the impact of the appropriate--or possibly any--positive ions, will be such as to necessitate a definite --and characteristically peristaltic--intermittency in the action of the neuro-fibril. We have imagined that the presence of the visual--or other--ions within the molecular tube of the neuro-
fibril—in the first instance, within the neural transmitter—by a mechanism already described brings about the production of a powerful positive charge surrounding this region of the fibril. One effect of this positivity is the propulsion of the exciting ions along the molecular tube; this is the primary effect resulting in the nerve impulse, but in the absence of any other change it would not suffice to establish a—more or less—continuous flow of visual ions towards the brain. We have supposed the positivity of the field surrounding an active neuro-fibril to be due to a physical change produced in this field by virtue of the presence within the molecular tube of the fibril of certain positive ions. These ions are pushed along ahead of the field which is produced on account of their own activity. Now if we admit that such stimulating positive ions have continuous access to the neural transmitter, we admit that only one batch of visual ions can be shipped along the fibril, for other ions following immediately after them would tend to produce a state of uniform positivity of the neurofibrillar field, so that the latter could obtain no grip—so to say—upon the ions themselves. It would be possible to generate an impulse only by bringing about some change in the ionic conditions existing at the neural transmitter, or at some other point in the fibre. This change is realized in many sense departments and in laboratory experimentation, but is apparently not necessary to visual sensation. The difficulty can be easily met: the production of a positive field about the neural transmitter will bring about a scattering of the positive and stimulating ions of the rods or cones outside of these transmitters. Continuous excitation thus becomes impossible; the impulse will necessarily be intermittent in character.
Our Hypothetical Nerve Impulse Is Not Perpetual Motion...........

A word may be said with regard to the energy changes involved in such a system as the one which we have described above. It is obvious that in its motion along the neuro-fibril the travelling ion would naturally be expected to encounter a considerable amount of resistance in the form of impeding molecules, and in overcoming this resistance in the course of its very rapid forward motion it must do a considerable amount of work, which should show itself in a heating effect—increased vibration of the neuro-fibrillar molecules. Now we must, of course, assume at the outset that the molecular conditions which the moving ion encounters within the neuro-fibril are by no means identical with those which impede ionic motion in ordinary liquids or solid. Says Gotch: "The special structure of nerve fibres is the undoubted basis for the high development in these of the attribute of conductivity, the natural and fundamental function of a living nerve, inasmuch as propagation is the purpose which the structure is especially framed to subservce." We must suppose that the relation which exists between the conditions of ionic movement in a neuro-fibril and in unorganized matter are similar to that which holds between the possibilities for the forward movement of any human individual in a dense crowd of people and along a well beaten path. Never-the-less there must be a considerable amount of resistance to overcome and hence some expenditure of energy will be necessary. This being the case a certain amount of heat should be produced in connection with the nerve impulse, and a certain amount of metabolism should be required to supply this liberated

(over)
energy. Well, it is obvious that our description of the nerve process, as we have pictured it, involves no chemical changes, but on this very account the mechanism suggested has the appearance of being a perpetual motion machine. Analysis will show, however, that this is not necessarily the case.

We have postulated a differential permeability of the nerve fibre material to positive and negative ions. The manner of the production of this differential permeability by the mere presence of the original travelling ion will not be discussed in detail. It may be attributed to the effect of this ion upon the electrical equilibrium of the tissue—to some slight modification of the position of molecular side chains, or of molecular orientation. On the other hand, it may be due to a chemical alteration of the tissues, catalyzed by the ion itself. In the latter case the alteration would not necessarily be of such a sort as to involve an appreciable expenditure of energy, and may be conceived to be immediately reversed under the influence of oxygen, the presence of which seems to be essential to the continuance of nerve activity—as soon as the catalyzing ion has passed on.

Howbeit, the absence of a heating effect due to the motion of the travelling ion, and the non-necessity of any supporting metabolism may be explained as follows. If we suppose a neutral mixture of positive and negative ions to be placed upon one side of a membrane which is permeable to the latter but not to the former, a certain number of the negative
ions will pass through the membrane, the result being the pro-
duction of a positive potential on the other side, a negative
potential on their side. The motion of any ion through the
membrane depends only upon its heat vibration. In passing through
the potential gradient represented by the membrane the velocity
of any negative ion will be decreased by the attraction which
is exerted upon it by the ionic mass which it is leaving. This
slowing of the heat motion of the ion is equivalent to a cooling
of the body of which the ion is a part, and thus the potential
difference which exists between one side of the membrane and
the other must be regarded as dependent upon temperature changes.
The electrical forces which govern the propagation of the tra-
velling ion along the nerve are generated only by virtue of a
slight cooling of the nerve tissue. The action of these forces
upon the travelling ion results in a thermo-dynamic process in
which the identical amount of heat is returned, the energy con-
ditions being left finally as they were in the beginning. There
is no perpetual motion because there is no actual gain of ener-
gy by the tissue. This explanation no doubt contradicts the
generalized second law of thermodynamics which implies the im-
possibility of generating differences in electrical potential
by cooling a body below the temperature of its surroundings, but
this law depends for its universal validity upon the existence
of equal freedom of movement for all of the bodily particles con-
cerned, and is known not to hold for small volumes. Our hypo-
thesis amounts to a suggestion that the nerve impulse presents
an exception to the law of entropy, and that it may be employed
in the disproof of the universality of this law, a consummation
devoutly to be wished.

The Advantages of the Above Hypothesis .... The advantages of the above described hypothesis of the nerve impulse are many. In the first place, it permits us to assume a uniformity of reaction of the nerve fibre to stimulation without assuming a uniformity in the nature of the impulse; viewed from the standpoint of the fibre alone the nerve impulse is simply an electrical peristalsis; this constitutes the only modification of the fibre in itself; but viewed as a whole the impulse is the peristalsis plus the ionic bolus which moves before it; as peristalsis, it is a specific energy, as a total process it is non-specific and its quality depends upon that of the immediate stimulus to the nerve. We thus become able to offer an explanation for the facts presented in visual and olfactory response without contradicting the fundamental principle that the manner of response of a tissue is determined by itself and not by the external force which acta upon it. On the basis of the above hypothesis we may easily comprehend the nature of the delay in the propagation of the nerve impulse which takes place in the synapses. At these places the neuro-fibrils discharge the travelling ions into free spaces; the process of fibre stimulation being repeated at each synapse. The diffuse structure of the dendritic processes of the neuron is admirably adapted to a collection and concentration of free ions which may be discharged in the vicinity of these processes by the axis cylinders of other neurons. Moreover in the case of complex synapses at which more than two fibres connect we may explain the probable differential reaction of these fibres to any axon stimulus which
comes into their midst by postulating the presence in the den-
dritic regions of the different fibres of special chemical sub-
estances which react with particular incoming ions in a specific
way, sometimes so that a relay impulse is produced, sometimes
so that none follows. On this basis it would be possible to
build up hypothetical nervous structures capable of explaining
even the most complex organic actions. Again, the hypothe-
sis of the nerve impulse here advocated permits a very simple
explanation of the induction of muscular contraction by motor
nerve currents. It is sufficient to suppose that the ionic con-
stituent of these currents is an oxidase or an oxidokinase, which
upon arriving at the muscle cell catalyzes the oxidative chemi-
cal reaction characteristic of muscular response; only a small
quantity of the enzyme would have to be transported, and being
small it would be rapidly destroyed. If we accept the
psycho-physical theory that affection and cerebral metabolism
are parallel, pleasantness being paralleled by anabolism and un-
pleasantness by katabolism, we may readily account for the affective
quality of the consciousnesses resulting from special com-
plexes of sensations—such as music—by referring it to the re-
actions of the many afferent ions; in certain cases there will
be synthetic processes, in others destructive processes. Har-
mony implies the flooding of the centers with ionic molecules
which react anabolically; disharmony depends upon the concentra-
tion of catabolically reacting combinations.

Certain Collateral Explan-
ations Offered by Our Hy-
pothesis.................

In addition to the above
mentioned paths of speculation
which are opened by our hypothe-
sis of the nerve impulse, there are certain explanations which
(over)
It may be noted that upon the hypothesis of the nerve impulse above suggested memory becomes a simple corollary of the inability of the brain cells to finally rid themselves of the foreign material thrust into them by the senses.
it affords of phenomena peculiar to the nervous system. Perhaps
the most important of these is the phenomenon of sleep. Sleep
appears to be principally determined by the inability of the
higher nerve centers—those mediating consciousness—to sustain
their activity; sleep consists primarily in an elimination of
the afferent impulses entering these regions. Upon our hypothe-
sis the necessity of this process can easily be understood; sen-
sation means the chemical drugging of the centers; for certain
periods the ionic material brought in by the afferent nerves can
be dissipated and oxidized with an effectiveness adequate to a
maintenance of the cortex in working order. Eventually, however,
it is necessary that the afferent currents be eliminated for a
time in order that a complete clearing of the tissues should be
brought about. We may suppose that one of the chief uses of oxy-
gen with reference to nerve activity is the destruction—probab-
ly outside the nerve substance itself—of the substances which
are carried along the fibre by the nerve impulse. If this is the
case we should expect the failure of the nervous structures due
to the deprivation of oxygen—as in the cutting off of the cir-
culation—to be centrifugal in its course; the higher centers, be-
ing foci of afferent discharge, will be most quickly fouled by
the foreign material. The Ritter-Valli law states this to be
the case; the functional failure of the nervous system after cir-
culation has been stopped, takes place according to the following
order: (1) the cerebral cortex, (2) the bulbo-spinal system, (3)
the central ends of the nerve trunks, (4) the outer ends of the
nerve trunks.

The hypothesis of the nerve impulse describ-

1 GOTCH, FRANCIS: art Nerve; in Schaefer's Text-book of Physiol.;
p. 477.
ed above obviously takes into account the fact that all conditions of nerve stimulation under laboratory conditions appear to be identical with those of electrolysis, or the production of ions in the nerve tissue. It is also in harmony with the facts which indicate the movement of a wave of electrical negativity along the surface of a stimulated nerve. This is the wave of superior permeability to negative ions which is induced by the travelling ion. The hypothesis is consonant with the fact that nerve fibres conduct equally well in either direction under laboratory experimentation, but that when performing their normal functions they apparently conduct in only one direction; a nerve impulse will proceed in whatever direction it is started. Experimental work upon nervous tissue tends to show that the processes of nerve conduction and nerve excitation are more or less distinct. This fact also is resumed in our hypothesis.

Olfactory Response and Our Hypothesis........... The instance of olfactory response has long been considered prejudicial to the doctrine of specific nerve energies. Apparently there is no end to the variety of sensation qualities which can be derived from differential stimulation of the olfactory nerve fibres. Yet the olfactory system is the most primitive of the sensory mechanisms. Now the olfactory nerve endings are peculiar in being the only sensory nerve terminations which are directly acted upon by the forces of the environment. Since the stimulus to olfaction is always chemical it becomes possible to suppose--according to the hypothesis which we have proposed--that every olfactory sensation quality is the direct psycho-physical result of the molecular transportation to the olfactory lobe of the stimu-
lating substance itself, or of some ionic component of this substance. The existence of unionizable odoriferous substances may be accounted for if we assume that the odor is to be attributed to impurities, characteristically present. Certain chemical writers have been led to express the opinion that no chemically pure substance is odorous.

The Concept of Impulse Intensity... Upon the basis of the above described hypothesis we may come to a somewhat clearer conception of the manner in which the visual impulse is dependent upon visual stimulation. It is clear that if that impulse consists merely in a movement of particular ions along the fibres of the optic nerve we may define the impulse intensity, \( \iota \), as the number of such ions passing any cross-section of the nerve fibre per second, and that we may define the density of the impulse, \( \sigma \), at any point in the length of the fibre as the number of ions in a unit of length (centimeter) in that region. Obviously, \( \iota = \sigma \bar{u} \), where \( \bar{u} \) is the velocity of the impulse. Now if we suppose the entrance of ions from the rod and cone segments into the fibrils to depend merely upon the chance encounter of these ions with the ends of the fibrils, the number entering per second will, on the average, be proportional to the concentration of the ions, so that we may write: \( \iota = k i_+ \), at the peripheral end of the nerve. It does not follow, however, that \( \iota \) will remain constant throughout the course of the impulse. In fact this is very improbable.

The Concept of Impulse Loss......... We should expect the resistance which is undoubtedly met by the ions in their passage along the nerve to result, in certain cases, in their
chemical destruction; in other cases they may unite with others of opposite charge, or may escape from the fibrils. This will result in a decrease in the impulse density, as the impulse passes towards the centers. At any particular point in the afferent course of the impulse this impulse loss will have a specific value, which may be defined as the number of lost from a unit length of the elementary visual conductor per second, so that if $\eta$ is the impulse loss, we have $\frac{\delta(\delta\zeta/\delta\gamma)}{\delta\gamma} = \eta$, where $\delta\gamma$ is an increment of length of the conductor in question. The impulse loss may be regarded as proportional at any point to the impulse intensity at that point. Since a differential of length is involved in the impulse loss, this proportionality must be written as $\eta = k_1 \zeta \gamma \delta\gamma$, the average being taken over the differential length considered. If $\gamma$ represents the distance of any point in the nerve from the point of stimulation—in the case of the visual impulse, from the retinal element—for every such point there will be a specific value for $\eta$: $\eta_\gamma$. The total impulse loss from one end of the nerve to the other will obviously be $\Sigma \eta = \Sigma_0^\kappa \eta \delta\gamma$, where $\kappa$ is the distance along the nerve fibre (elementary conductor) from the retinal cone (or rod: retinal element) to the cerebral cell (or cells: cortical element) supporting C. The total impulse loss will be proportional to the average of the impulse intensity taken along the entire length of the conduction path, thus: $\Sigma \eta = k_1 \left( \frac{1}{\kappa} \Sigma_0^\kappa \zeta \delta\gamma \right)$. It will also be proportional, with a different constant, as $k_1^1$, to the impulse intensity at any specific point in the elementary conductor. In our discussion we shall employ the constant $k_1^1$—which is constant only with respect to changes in $\zeta$, and not to changes in $\gamma$—
with reference to the impulse intensity at the cortex, so that
\[ \Sigma \eta = k_i \zeta_0. \]

Places of Greatest Impulse Loss..... It may appear from the above discussion that we regard impulse loss as determined merely by the intensity of the impulse. This, however, is not actually the case; \( \eta \) is dependent upon at least two factors, the one mentioned and another which we may call the neural confining force. If this force is \( f \) at any point the impulse loss will be proportional to \( (\zeta / f) \). Now \( f \) must vary from point to point, and must depend upon the structure of the neural conductor. It will be by far the smallest at the synapses. Hence the impulse loss will undoubtedly be greatest in these regions, where the travelling ions are discharged into the open synaptic spaces, only a limited number of them entering into the relayed impulse which is generated in the contiguous neural transmitters of the adjoining neuron. In the case of the visual impulse the greatest value of \( \eta \) will without doubt be that which it possesses within the retina itself, especially in the inner and outer molecular layers (cf. page 154). Definite losses will also occur in the synapses of the corpora geniculata externa, in the direct visual path to the cortex. Extra-synaptic losses are probably negligible.
Section XXII : The Visual Impulse and the Visual Cerebrosis.

Visual Cerebrosis is Merely a Concentration of the Impulse.

With regard to the nature of the visual cerebrosis and its dependency upon the visual impulse we shall make only the simplest assumptions. In a following Part (page 265) we shall discuss the impulse itself more in detail, making specific assumptions concerning the number of molecular resonators present in the cone cells, the necessary correlation of their activities with the specificity of the impulse, the relation of the elements of the impulse with the cortical process, and, finally, the psycho-physical parallelisms which may be held to exist between the cortical processes thus described and the modifications of the visual field. At present it is sufficient to point out the general nature of the hypothetical and mathematical relationships which we shall suppose exist between the visual impulse and the visual cerebrosis.

We have described the visual impulse as a flow of certain ions along the fibres of the optic nerve. These ions are of several kinds—corresponding with the different species of molecular resonators which are present in the rods and cones—and they are carried in the neurofibrils of the nerve fibres. The intensity of the impulse moving in any fibre is determined by two factors, the concentration of ions in the end cell and the loss in transit. We suppose that the conducting fibres are connected with certain cells of the visual cortex of the cerebral hemispheres; for each conducting fibre there is a special cortical cell or group of cortical cells, and into this cell or these cells this fibre pours its flood of visual ions. We shall define the
visual cerebrosis, C, as the ionic state of the visual cortical cells--the cells of the cuneate region of the cerebral hemispheres (cf. page 61). In other words the only difference which we shall conceive to exist between the visual cerebrosis and the visual impulse is a quantitative difference; the visual cerebrosis is a cortical concentration of the visual impulse, for this reason, and, in this way, is determined both qualitatively and—in part—quantitatively by the impulse.

Let us define the intensity of the visual cerebrosis, c, as the concentration of visual ions in any element of the visual cortex. By an element of the visual cortex we mean the structural unit functional modifications of which are paralleled psycho-physically by elementary visual sensations (cf. pages 115 & 232). This concentration measure may be expressed in terms of ions per cortical element. We shall see later that there are probably several varieties of visual ion, and hence that c is probably complex, but this contingency need not trouble us here. Now the value of c for any cortical element will vary with the time, but it must obviously be representable as a function of several other variables besides the time, such variables as the intensity of the incoming visual impulse (elementary) and the rate of dissipation of the visual ions from the cortical element in question. If we make the only reasonable assumption, viz., that this latter rate is itself a function of the concentration, and is, in fine, proportional to it, we may express the relation existing between the value of c and that of \( c' \), the intensity of the visual impulse arriving at the cortical element at any instant, in the following way:
\[ c_{t_1} = c_{t_0} + \sum_{t_0}^{t_1} (c_{t} - k_c c_{t}) \Delta t \]

where \( c_{t_1} \) represents the concentration of visual ions in the cortical element at the time \( t_1 \), \( c_{t_0} \) the same at the time \( t_0 \) and \( c_{t} \) represents the concentration (intensity of the visual cerebrosis) at the time \( t \) which varies in the integration process. \( c_{t} \), also, is the intensity of the visual impulse at the cortical element at the integration time. We shall call the constant \( k_c \) the cortical dissipation coefficient, and the quantity \( \varphi = k_c c \) the cortical dissipation. Even assuming \( c_{t} \) to be a constant, the integration of the above equation is not easy, and no attempt will be made to derive the integral in this thesis. However, at another point (page 299), we shall find the above expression of value in the explanation of certain phenomena connected with the relative durations of stimulus and sensation.
PART EIGHT: AN ACCOUNT OF CERTAIN DETAILS OF THE HYPOTHETICAL VISUAL MECHANISM.

Section XXIII: The Exact Psycho-physics of the Element-Visual Sensation.

An Analysis of the Relation: \( S = f(C) \)

In this Section it is purposed to make certain qualitative and quantitative assumptions amounting to an analysis of the psycho-physical relationship expressed in the function: \( S = f(C) \). In our psychological study of the elementary visual sensation, \( S \), we found that this sensation was capable of exhibiting six fundamental attributes (cf. page 95), redness, yellowness, greenness, blueness, whiteness and blackness. These we indicated qualitatively by the symbols, \( R, Y, G, B, W, \) and \( B \), and quantitatively by the symbols, \( r, y, g, b, w, \) and \( \bar{b} \) respectively. It was stated that a complete description of any elementary visual sensation could be given in terms of these variables, and certain ideational variables. In addition to the six fundamental attributes, three derived attributes were distinguished; these consist in combinations of the fundamental attributes. Now it is obvious that if we desire to throw the qualitative relation, \( S = f(C) \), into quantitative form, it will be necessary to express \( S \) in terms of the variables, \( r, y, g, b, w \) and \( \bar{b} \), and thus to split the function \( s = f(c) \) into six component functions, as follows: (1) \( r = f(c_r) \), (2) \( y = f(c_y) \), (3) \( g = f(c_g) \), (4) \( b = f(c_b) \), (5) \( w = f(c_w) \) and (6) \( \bar{b} = f(c_{\bar{b}}) \). Having performed this operation we find ourselves forced to postulate the presence in the cortical element \( Z_c \) (cf. page 233) six distinct ionic concentrations (cf. page 250), that
is, we must admit the presence of six qualitatively distinct sorts of ions, which we may designate as \( C_r, C_y, C_g, C_b, C_w, \) and \( C_{b} \).

The Relation Between \( C_w \) and \( C_b \) .......... In our examination of the relations existing between the different attributes of the elementary visual sensation (page 95), we found it possible to write: \( b = b_m - w \), where \( b_m \) was a constant, provided the tint, \( t \), remained constant. This relation makes it possible for us to regard \( C_b \) as the absence of \( C_w \). That is, instead of asserting that \( C_b \) is a special cortically present ion, we may state that \( C_b \) is the cortical state or process which consists in an absence of ions; it is a negative ionic state. Although somewhat similar relations exist between the hue measures for specific sensations, these relations (cf. page 96) are not such as to permit the assumption that the state corresponding with the presence of one of the hues is merely the absence of the state corresponding with the presence of another. The reason is that none of the hues are constantly correlated; absence of yellowness does not necessitate greenness or redness or blueness in particular, even with high chroma; it merely necessitates some one, or some possible combination of these. On the other hand absence of whiteness with high tint, absolutely necessitates blackness; hence it becomes possible to regard the cortical state paralleled by blackness, as that state which obtains in the absence of the state paralleled by whiteness. Since when the chroma of \( S \), \( h \), is zero, the values for \( r, y, g, \) and \( b \), are all zero and the tint, \( t \), is a maximum, \( C_b \) may also be regarded as the cortical state corresponding with the absence of all of the hues as well as the absence of whiteness.
Since in accordance with our theory of the visual impulse only positive ions can be regarded as reaching the cortical elements via the fibres of the optic nerve, and since we have postulated no other means whereby the ionic content of these elements can be qualitatively modified, we are forced to define five visual ions—which are brought to the cortex in the visual impulse—as follows: \( c_r = I_{r+} \), \( c_y = I_{y+} \), \( c_g = I_{g+} \), \( c_b = I_{b+} \), and \( c_w = I_{w+} \). Correspondingly, the five ionic concentrations are: \( c_r = i_{r+} \), \( c_y = i_{y+} \), \( c_g = i_{g+} \), \( c_b = i_{b+} \), and \( c_w = i_{w+} \).

In order to expedite discussion, we shall assume that the elementary psycho-physical functions: \( r = f(c_r) = f(i_{r+}) \), etc., given on page 252 may be written as follows: (1) \( r = i_{r+} \), (2) \( y = i_{y+} \), etc. The writer believes that in all probability direct psycho-physical relationships are of such a character that when formulated mathematically they become strict proportionalities. Whether or not this belief is justified is a question the answering of which would require a great deal of investigation. If, however, the assumption should lead us astray, in its present application, it may readily be dropped without vitiation of the balance of our argument.

Since in this discussion of the psycho-physical relations of the elementary visual sensation, \( S \), we have eliminated the ideational element of the visual consciousness, it is hardly necessary for us to indulge in any lengthy consideration of the psycho-physics of the visual consciousness in general.
However, a few words upon that subject may not be out of place. Parallel with the visual consciousness as an integral there must be an integral cortical excitation. Just as the many elementary visual sensations are combined to make up the visual field, so the elementary visual cerebroses must be combined to form a systematic cerebral process. There can be little doubt that the structural elements supporting the elementary visual cerebroses are individual cortical neurons or groups of neurons. Some difficulty may be felt in accepting the view that the visual consciousness, which is so integral a thing, is dependent upon the physiological conditions of separated elements such as the cortical nerve cells appear to be. But this difficulty must inevitably be met, for there can be no doubt that consciousness must, upon experimental grounds, be subdivided and its parts assigned to different regions of the brain, even those widely separated from each other. At bottom the difficulty is illusory, for the neurons are not actually discontinuous; the physiological and ionic status of one neuron in an excited system is merely a conceptual part of a process which is in its final physical nature to be thought of as integral. Consciousness is based upon the physiological contents of a cortical synergy; the character of the neurons (perikarya and processes) involved in this synergy determine the consciousness at any instant. Most writers upon psycho-physics appear to hold that the so-called processes of consciousness must necessarily be paralleled psycho-physically by chemical changes, or something obviously kinetic or dynamic in nature. So far as the basic principles of psycho-physical argument are concerned, however, C in our problem may with equal
justification be regarded as a state or as a process. We have chosen to define it as a state, a state of ionization, but ultimate physical analysis of this state would show that at bottom it is a process; modern physical thought tends more and more to regard all phenomena as expressions of processes rather than states; if we so desired, we could undoubtedly write 0 as a time derivative; it is more convenient, however, to describe it in static terms. The cerebral synergy, of which 0 is a part, may be regarded as depending for its unity upon the electrical state of the particular neurons concerned. Electric and magnetic fields are physical factors which are not only non-atomic in character, but which are capable of inter-fusion and reaction in such a way as to make a single system out of many otherwise isolated elements. A complex electrical field presents many characteristics which are comparable—by psycho-physical analogy—with those of a field of consciousness (cf. page 83). It is obvious from the above remarks, that in this thesis we shall not consider the cortical position of any cortical element involved in the visual synergy as necessarily of importance in determining the position of the sensory attributes paralleled by its activity, in the visual field. The visual field is not paralleled by the geometry of the cuneate cortex, but by the connections of the neurons of that region. The visual field represents a system, not a plenum. A single point in the visual field may be represented in the cortical system by any number of neurons, but if so all of these neurons possess identical connections with the other neurons which may possibly be involved in the synergy. Any neural synergy may be regarded as spatially defined by the continuous extent of an elec—
by the continuous extent of an electrical field; it involves the existence of free lines of electrical force, and the terminations of such lines of force determine the boundaries of the synergy. When we speak of the visual synergy we mean that synergic system dependent upon the functioning of the retina and the optic nerve, which is a part of the greater synergy paralleled by consciousness as a whole. There must be many lesser visual synergies which are only paralleled by "sub-conscious" psychoses, if by any.
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Section: XXIV : The Details of the Visual Mechanism in the Cortex.

The Cortical Receiver.... In the foregoing Section we have postulated the existence in the visual cerebral cortex of five distinct species of ion corresponding psycho-physically with the five fundamental attributes of the elementary visual sensation, -- if we except the element of blackness. These ions were $I_{w^+}$, $I_{r^+}$, $I_{y^+}$, $I_{g^+}$ and $I_{b^+}$, and the postulated psycho-physical relations were as follows: (1) $r = i_{r^+}$, (2) $y = i_{y^+}$, (3) $g = i_{g^+}$, (4) $b = i_{b^+}$, and (5) $w = i_{w^+}$, where $i_{r^+}$, etc., represent the intensity of the visual cerebrosis as regards the particular ion designated (cf. page 254).

It is now our task to consider a little more in detail the conditions determining these quantities. It has been intimated that the five ions mentioned above are to be looked upon as components of the visual impulse, and that their presence in the cortical elements is to be attributed to their actual transportation to these elements via the fibres of the optic nerve. This we shall hold to be the case except in the particular instance of the ion $I_{w^+}$, as will shortly be explained. Now the remaining four ions--and possibly others--we suppose to be convected along the optic nerve fibres from the visual end-organ in a way already described (cf. page 235) and which will later be given still further consideration (cf. page 265). Now the first cortical element into which the elementary visual impulse passes in its afferent course, we shall call the cortical receiver, to be designated by means of the symbol $Z_{ov}$. 
$Z_{cv}$ may be a single neuron or a system of neurons; whatever the case, everything which happens within pertains to the elementary visual response, and it is itself an elementary cortical receiver.

The Luminosity Element...... In addition to the cortical receiver we shall postulate the existence of several other cortical elements correlated psycho-physically—in their functioning—with the elementary visual sensation. The first of these to be considered is an element which we shall denominate the cortical luminosity element, because its functioning is paralleled by the attribute of sensory luminosity. We will suppose that the material of this element—which may be a single neuron or a system of neurons—includes a substance which has a high normal ionization, the two ions into which it is broken up being $I_{w-}$ and $I_{w+}$, respectively. This $I_{w+}$ is to be considered identical with that postulated above as the determinant of the sensory attribute $W$. Now we will suppose that the cortical luminosity element—which may be symbolized by $Z_{cl}$—and the cortical receiver ($Z_{cv}$) are separated, or connected, by an osmotic membrane—or a similarly operating physiological mechanism—which is permeable to the negative ion ($I_{w-}$) but not to the positive ion ($I_{w+}$). We may imagine this differential permeability to depend upon a great difference in the sizes of the two ions. The manner in which the apparatus here pictured will operate under the influx of the visual impulse is obvious. Presumably the positive ions: $I_{r+}$, $I_{y+}$, $I_{g+}$, and $I_{b+}$ are of the same order of magnitude as $I_{w+}$, and hence will not pass through the membrane. Upon the arrival of any of these four ions of the impulse in the cortical receiver, a potential gradient will be established
between \( Z_{cv} \) and \( Z_{cl} \) of such a character that the positive ions will tend to pass through the membrane from \( Z_{cv} \) to \( Z_{cl} \), while the negative ions \( (I_{w-}) \) will tend to pass in the opposite direction. The latter process is the only one which can occur, and if it takes place the cortical luminosity element will left with an excess of positive \( I_{w+} \) ions, the condition of the proportional appearance of the attribute \( W \) in the parallel elementary sensation. If \( i_{w+} \) is the concentration of unbalanced \( I_{w+} \) ions in the luminosity element, we have: \( w = i_{w+} \).

In addition to the cortical luminosity element, \( Z_{cl} \), we shall postulate the existence of four other specific cortical elements connected with visual response. These four remaining elements we shall designate as the cortical chromatic elements. We shall imagine them to be connected with—or separated from—the cortical receiver by four specific selective membranes—or equivalent neural mechanisms—through which but one of the four ions, \( I_{r+} \), \( I_{y+} \), \( I_{g+} \), and \( I_{b+} \), of the visual impulse can pass in each case. We shall name and symbolize these elements as follows: (1) the R-element = \( Z_{cr} \), (2) the Y-element = \( Z_{cy} \), (3) the G-element = \( Z_{cg} \), and (4) the B-element = \( Z_{cb} \). \( Z_{cr} \) receives only ions of the type \( I_{r+} \), \( Z_{cy} \) ions only of the type \( I_{y+} \), etc. The concentration, \( i_{r+} \), of \( I_{r+} \) ions in \( Z_{cr} \) corresponds with the attributes of the elementary sensation, \( S \), in such a way that \( r = i_{r+} \). Similar relations hold psycho-physically for the remaining chromic elements, their respective ions, and the hues, \( Y, G, \) and \( B \). Each chromic element may be regarded as a single neuron or as a system of neurons. Should no reason arise for another view, we
shall consider each of the cortical elements above defined—
$Z_{cv}$, $Z_{cl}$, $Z_{cr}$, etc.—as a single neuron—perikaryon and pro-
cesses, -- but this question is not raised by the above defini-
tions.

Relation of the .. Each of the six cortical elements
to the Visual Syn-
ergy.............. defined above is to be considered an

instrument in the induction of the attrib-
utes of a single elementary visual sensation, $S$, that is, their
functioning involves the presence of hue or luminosity only at
a single point in the visual field. However, only five of these
elements are to be regarded occupants of the visual synergy.
The cortical receiver is not involved in the visual synergy.

If difficulty is felt in reconciling what has been said on page
255 with regard to the conditions of inclusion within the visual
of any neuronic activity, -- with the statement just made, one
may assume that the ionic membranes, the existence of which we
have postulated, are actually something more complex than a sim-
ple osmotic mechanism, and that the forces directing the move-
ment of the several visual ions are not simply those existing
by virtue of the differences in the concentration of positive
and negative ions in the separate cortical cells. We have postu-
lated a chemical selective mechanism on page 245. However,
the writer believes that the difficulty can be met in some other
way.

We shall give an evolutionary explanation of the devel-
opment and physical utility of the above described visual cor-
tical apparatus in our Part on the evolution of the visual mech-
anism (cf. page 431f).
On pages 250 and 254 we have defined several quantitative terms dealing with the visual cerebrosis. The meaning of cerebrosis intensity, \( c \), in connection with the above postulated cortical mechanism is obvious. This term must evidently be split into five components, one corresponding with each of the five visual ions, \( I_{r^+} \), etc., to \( I_{w^+} \), which we have assumed to exist in the visual synergy. Outside of the synergy --in the cortical receiver--are to be found the four "chromic" ions, the ion \( I_{w^-} \), and another shortly to be mentioned, \( I_{w^+} \). The concentrations of these ions in the cortical receiver may be distinguished from those involved in the visual synergy by the denotation: initial cerebral intensity, \( c' \). In addition to the intensity terms, we have mentioned a cortical dissipation term, \( \psi \); clearly the dissipation of each of the ions concerned may be considered separately, both as regards the synergic and extra-synergic concentrations. Thus we have: \( \psi_r \), \( \psi_y \), \( \psi_w \), etc. Obviously, upon the hypothesis which we have outlined, part of the dissipation of the initial cerebral intensity goes into the production of the cerebrosis intensity. With respect to the cortical luminosity element we may find it necessary to postulate a recuperation process to replace the ionic material lost through dissipation.
N.

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Section XXV : The Components of the Visual Impulse.

We have defined several terms characterizing the visual impulse (page 246).

The most fundamental of these is $I$, which designates the qualitative attributes and contents of the impulse viewed as a whole. From the quantitative standpoint the impulse is characterized by a definite intensity, $I$, at every point in its course; a corresponding density, $\sigma$; a velocity, $\bar{u}$; and an impulse loss, $\gamma$.

It is now our purpose to briefly indicate the analysis of the term $I$ which is necessitated by the line of speculation which we have chosen, and to point out the results of this analysis for the quantitative consideration of its characters.

The Component Quantitative Terms of the Visual Impulse ......

We have postulated the possible arrival in the cortical receiver, $Z_{cv}$, of at least four chemically distinct ions: $I_{r+}$, $I_{y+}$, $I_{g+}$, and $I_{b+}$. To these we will now add a fifth, viz., $I_{w'+}$; this we shall call the complementation ion; its function and its evolutionary significance will be explained later (cf. pages 270 and 437). In accordance with our conception of the physical nature of the visual nerve impulse and of the relation existing between the initial visual cerebrosis (that, in $Z_{cv}$) and that impulse, we must suppose that these ions are convected into $Z_{cv}$ via the optic nerve fibres from the retina. Hence it becomes necessary to analyze the impulse--at least, if we view it generically--into five components, such that: $I$ (generic) = $I_{r+} + I_{y+} + I_{g+} + I_{b+} + I_{w'+}$. From this it becomes clear that at any point in the course of the impulse five specific components of the general impulse intensity, $I$, 

may be described, symbolizing the number of ions of the several respective species passing that point per second, or—to emphasize the differential aspect of this measure—symbolizing $\overline{u} \times \sigma$, the impulse density or the concentration of each ion at the point. Let us designate these five component intensities by the symbols: $\zeta_r$, $\zeta_y$, $\zeta_g$, $\zeta_b$, and $\zeta_{w'}$, respectively. Similarly, we have five component impulse losses: $\gamma_r$, $\gamma_y$, $\gamma_g$, $\gamma_b$, and $\gamma_{w'}$. It is conceivable that in the case of ions conducted along different nerve fibres that specific velocities should exist; such velocities may be designated in accordance with the convention: $\overline{u}_{w'}$. 
Section XXVI : The Number and Properties of the Molecular Resonators.

The Chromatic Resonators of the Cones From the foregoing analysis of the visual impulse the primary details of our hypothesis with regard to the retina may readily be deduced. Since psycho-physical experiment makes it clear that the hues, R, Y, G, and B, are quantitatively correlated with the wave-length, \( \lambda \), of the stimulating light, so that \( r = f_r(\lambda) \), \( y = f_y(\lambda) \), \( g = f_g(\lambda) \), and \( b = f_b(\lambda) \) --it immediately becomes necessary to assert that the visual ions, \( I_{r+} \), \( I_{y+} \), \( I_{g+} \), and \( I_{b+} \) are those resulting from the ionic dissociation of four special molecular resonators, which we will--for the time being, at least--call: \( M_r \), \( M_y \), \( M_g \), and \( M_b \), respectively. These resonators react with the stimulating light in a manner which we have already described in great detail (cf. pages 177 and 190). Now we shall, in the first instance, postulate the existence of the above described resonators only in the cones of the retina, and we shall not assert that all of the cones possess all of the resonators, but only that some of them possess them all. These resonators we shall speak of collectively as chromatic resonators, not meaning, necessarily, that they are colored but that they are the retinal mechanisms mediating the hues of the elementary sensation.

The Achromatic Resonator of the Rods.......... In addition to the four chromatic resonators assumed above, we shall posit the presence of a fifth molecular resonator, which does not occur in the cones at all, but is found only in the rods. This we shall designate as \( M_w \), which we shall denominate
- the achromatic resonator, and which we shall hold to be identical with the visual purple (cf. page 386).

The Problem of the Specific Quantitative Properties of the Resonators...

Now each one of the five molecular resonators the existence of which we have postulated, possesses certain definite quantitative characteristics, which must be specified in any attempt to present an accurate--or even a useful--hypothesis of visual response. In the unstimulated rod and cone segments each of the resonators, \( M_R \), \( M_Y \), \( M_G \), \( M_B \), and \( M_W \), is present in a certain concentration; \( m_R \), \( m_Y \), \( m_G \), \( m_B \), \( m_W \), respectively. Each, moreover has a specific normal ionization, quantities which may be designated by the symbols: \( \gamma_R \), \( \gamma_Y \), \( \gamma_G \), \( \gamma_B \), and \( \gamma_W \). Each possesses a specific resonance gradient for every wave-length, this gradient being governed by a specific resonance function. The resonance gradients of the several resonators for any wave-length, \( \lambda \), and unit light intensity, may be represented by the symbols: \( \rho_{R\lambda} \), \( \rho_{Y\lambda} \), \( \rho_{G\lambda} \), \( \rho_{B\lambda} \), \( \rho_{W\lambda} \), and the corresponding resonance functions by: (1) \( \dot{m}_R = f_{R\lambda}(\lambda) \), (2) \( \dot{m}_Y = f_{Y\lambda}(\lambda) \), (3) \( \dot{m}_G = f_{G\lambda}(\lambda) \), (4) \( \dot{m}_B = f_{B\lambda}(\lambda) \), and \( \dot{m}_W = f_{W\lambda}(\lambda) \). (cf. pages 213 & 310). In addition to the above-defined specific properties we have to consider the light sensitivity, \( q \), peculiar to each resonator. These specific light sensitivities will be symbolized by: \( q_R \), \( q_Y \), \( q_G \), \( q_B \), and \( q_W \), respectively. Moreover, it is probable that each resonator is metabolically supported by specific aesthesogenases and aesthesogens. The respective aesthesogens will be symbolized—as indicated on page 219—by the conventions, \( \overline{AB}_s \) and \( \overline{CS}_s \), where \( s \) is the appropriate subscript; the corresponding concentrations will be
represented by \( \overline{ab_s} \) and \( \overline{c_s} \). We shall designate the respective aesthesogenases by prefixing the letters, R, Y, G, B, and W' to the word aesthesogenase, thus: W'-aesthesogenase. The specification of the exact—or approximate—nature and values of the constants of visual stimulation above defined constitutes a part of the problem of the explanation of the peculiarities of the elementary sensation, S, and its relation with other similar sensations in the visual field. We shall therefore postpone attempts to assign numerical or proportional values to these constants until we come, in Part Nine to a brief consideration of the manner in which our hypothesis may be employed in the explanation of the manifold phenomena of visual response.
Section XXVII: The Mechanism of Complementation.

The Complementation Molecules......... In order to account physiologically for certain cardinal facts of the psycho-physics of visual response, we shall make the following addition to our hypothesis of the visual mechanism. Within the large "ganglion" cells of the inner strata of the retina there exists a large supply of a certain substance which we may designate as the complementation substance. This substance is probably present only in those cells which are connected with the retinal cones. The component molecules of this complementation substance are made up a nucleus and two side chains. Each of these side chains is a potential negative ion, the nucleus itself being a doubly charged positive ion. Of these molecules there are two varieties. The first is so constructed chemically that its two negatively charged ionic side-chains are capable of combining simultaneously with the two positive ions of the visual impulse: \( I_{r+} \) and \( I_{g+} \). The second reacts in a similar way with the visual ions: \( I_{y+} \) and \( I_{b+} \). The result is that in each case the positively charged nuclei of the molecules are set free and become a part of the impulse. It is impossible that the side-chains of the complementation molecules should be replaced—or removed—separately, or by reaction with ions other than those specified. We shall speak of the two molecules above described as the R-G-complementation molecule, and the Y-B-complementation molecule, respectively.

The Mechanism of the Complementation Reaction..............

The mechanism of the complementation reaction may be imagined as follows.

Let us symbolize the R-G complementa-
tion molecule as: \( w_{crw} = I_{r-} (I_{w'}^{++}) I_{g'}^+ \). The reaction:
\[ I_{r+} + w_{crw} \rightarrow (I_{r+} I_{r-}^*)((I_{w'}^{++}) I_{g'}^- + I_{g'}^+ \]
first occurs. The substance produced is very unstable, and is constantly breaking down again, by the reverse reaction, into \( w_{crw} \) and \( I_{r+} \). However, the following reaction is also possible: 
\[ (I_{r+} I_{r-}^*)((I_{w'}^{++}) I_{g'}^- + I_{g'}^+ \rightarrow I_{r+} I_{r-}^+ + I_{w'}^{++} + I_{g'}^+ I_{g'}^- \]. The first and last compounds written in this equation are not the same as the molecular resonators, \( W_{r} \) and \( W_{g} \), and they are to be considered as wholly unionizable in nature. The ion \( I_{w'}^{++} \) enters into the visual impulse and is identical with \( I_{w'}^+ \) of our previous discussion. An exactly analogous reaction may be imagined as occurring between the visual ions \( I_{y}^+ \) and \( I_{b+} \) and the Y-B-complementation molecule: \( W_{cyb} = I_{y}^- (I_{w'}^{++}) I_{b}^- \). As before the liberated ion, \( I_{w'}^{++} \), enters into the visual impulse, and is to be considered identical with \( I_{w'}^+ \). Whether these ions are actually the same makes no particular difference so far as the results of our hypothesis are concerned.

Physiological Relationships of Our Complementation Molecules......

It will be perceived that the molecular complementation process above described is essentially the same as that of Freytag's hypothesis (cf. page 136); it amounts to a chemical interpretation of Freytag's view, which is that either a "warm" or a "cold" visual impulse may pass through the ganglion cells but not both simultaneously. But besides comparing our hypothesis with that of Freytag, we may assimilate it to another well known physiological theory. The complementation molecule the existence of which we have postulated is a body of the same general chemical character as an Ehrlich amboceptor, or cell re-
ceceptor of the third order. If we are to believe the teachings of Ehrlich and his school, substances of this sort are readily produced by the cells of the body. We have supposed the complemen-
tation reaction to occur in the ganglion cells of the retina for the reason that these cells, being of such large size and so strongly nucleated, may well be conceived to support some de-
finite metabolic function, and also because of the fact that the process underlying color complementation appears from experiment to be of a retinal rather than a cerebral nature. It is quite possible, however, to suppose that the complementation substance may, when necessary, be produced by the cell which we have desig-
nated (page 254) as the cortical receiver, since amboceptors--
or substances acting in a similar manner--seem to be easily gener-
at by the cells of the organism as a whole, to meet the most specific of demands. In our discussion of the evolution of the visual mechanism we shall elucidate the function and manner of development of the complementation reaction.

Quantitative Effects .
The quantitative effects of the
of the Complementation
reaction upon the visual
Reaction on the Constit-
tution of the Impulse.
retinal ganglion cells may briefly be indicated. Making use of
the terminology already established (cf. page 266), if \( \zeta_a \) and \( \zeta_k \)
are the intensities of two complementary ionic components of the
visual impulse previous to its arrival at the ganglion cell, and
if \( \zeta_a > \zeta_k \), we have, for the same components after passing the
ganglion cell: \( \zeta'_k = 0 \); \( \zeta'_a = \zeta_a - \zeta_k \); and, also, \( \zeta_w = 2 \zeta_k \).
This entire discussion applies only to the impulse which origi-
nates in the cones. In the case of the rods, there is at the out-
(over)
set but a single impulse component, viz., $I_{w'^+}$, which is the product of the ionization of the achromatic resonator (cf. page 267) $M_{w'}$. As we have said before, it is immaterial whether the various ions which we group under the common designation, $I_{w'^+}$, are identical or not, because, as we shall point out more clearly later on, the only thing about them which is of importance is the magnitude of their charge. We shall find it convenient to speak of $I_{g^+}$ and $I_{r^+}$ as complementary ions; $I_{r^+}$ is complementary with respect to $I_{g^+}$, and vice versa. A similar application of this terminology may be made to the ions $I_{y^+}$ and $I_{b^+}$. The ion $I_{w'^{++}}$, on the other hand, is the complementation ion.
PART NINE: THE EXPLANATION OF CERTAIN VISUAL PHENOMENA.

Section XXVIII: The Electrical Phenomena in the Stimulated and Unstimulated Eye.

Purpose of This Part of the Thesis... It is now purposed to enquire to what extent and in what way it is possible to explain many of the facts of visual response by the use of the hypotheses which are now current or which have been outlined in this thesis. Our task is two-fold: the criticism of extant hypotheses according to their power to systematize the manifold of visual phenomena; and parallel with this an indication of the manner in which the assumptions and conceptions which we have carefully outlined in the preceding pages may be employed in the accomplishment of the same end. Owing to the limited amount of time at the disposal of the writer, these criticisms and explanations will of necessity be somewhat sketchy in character.

The Electrical Condition of the Unstimulated Eye... Since the line of thought which we have followed in our attempt to describe the mechanism underlying visual sensation has depended to a great extent upon the utilization of concepts of electricity, it will be interesting, in the first place, to determine whether or not our postulates are in harmony with certain objectively—or, better, physically,—demonstrable electrical states and changes of the eye. Let us first take notice of the electrical condition of the unstimulated eye. We have supposed that the rods and cones of the retina are the seats of the production of an equal number of posi-
tive and negative ions, and that, of these ions, the former are propagated along the optic nerve in the form of the visual impulse (cf. page 237). It follows that the negative ions remain in the bacillary layer. Since the state of ionization at the retina is not quantitatively zero even in the absence of all light stimulus (cf. page 217), it follows that if we examine a fresh and even unstimulated eye we should find the cut surface of the optic nerve to be positive with respect to the layer of rods and cones, the latter being negative. Experiment shows this to be the case.\(^1\) Now we have seen that by reason of the fact that the travelling ions are discharged entirely from the neuro-fibrils at the open spaces which we call synapses—to be picked up again by the neural transmitters of contiguous neuro-fibrils—there should be a high impulse loss in synaptic regions (cf. pages 154 and 248). The inner layers of the retina include two important strata of synapses (the inner and outer molecular or plexiform layers). In these regions practically all of the ions which have been transported along the rod and cone fibres (and the bi-polar cell fibres) from the bacillary layer, are set free. Many of these ions are taken up by the fibrils of the optic nerve fibres proper, but others are definitely lost into the ocular media. On account of this loss we should expect to find a smaller concentration of these positive ions in the optic nerve than in the retinal synapses; that is, experiment should show—if our hypothesis is defensible, that the synaptic regions of the retina are normally positive with respect to the cut surface of the optic nerve. Experiment does demonstrate this to be the case.\(^2\)

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1 W.H.R.R. p. 1050  
2 W.H.R.R. p. 1051.
It follows from the above discussion that if the inner and the outer strata of the retina are compared, the former should be positive, the latter negative. This is a direct result of our conception of the visual impulse, and it is verified by experiment. When the optic nerve is connected with the cornea of the eye the current passes from the cornea to the nerve. This positivity of the cornea is to be attributed to the effect of the positive ions which escape from the visual fibrils in the retinal synapses. On account of the electrical forces acting between the ions, we need not be surprised at the occurrence of an impulse loss comparable in magnitude with the residue of ions which are picked up by the optic fibres. On the other hand—as we should expect—the sclerotic coat of the eye is negative with respect to the nerve, the sclerotic being charged with ions derived from the outer—rod and cone—layers of the retina, and which are therefore negative.

**Electrical Changes In the Eye Under the Action of Light**

Suppose that light is permitted to fall upon the retina. According to our postulates there should be an immediate increase in the ionization of the molecular resonators which are located—-it will be recalled—-in the rod and cone layer. The consequence is an increase in the impulse intensity, an increased impulse loss in the synaptic strata, and an increased positivity of the optic nerve endings. If the entire retina is illuminated, the first electrical effect will be an increase in the negativity of the bacillary layer owing to the departure of a larger number of positive ions per element of time. The

1 W.H.R.R., p. 1051. 2 loc. cit.
second electrical effect will be an augmented positivity of the synaptic layers, owing to the discharge of the above mentioned positive ions into this region. These ions will in part be picked up by the fibrils of the optic nerve fibres with the result that an increased positivity of the cut surface of this nerve will ensue. Coincident with this, however, there will be a still greater enhancement of the positivity of the ocular media and hence of the cornea, by virtue of the increased impulse loss and the electrolytic connection existing between the cornea and the highly positively charged inner retinal surface. We expect therefore that the incidence of light at the retina will result in a positive variation of the current normally established between the cornea of the eye and the cut surface of the nerve. Our expectation is verified by experimental results. It is said that when the isolated retina is employed, this positive variation is followed immediately by a negative variation. According to Kühne and Steiner this is to be attributed to injury to the retina, as when the latter is in the best condition, the negative variation is small, while when the entire eye is employed this variation is absent altogether. If Kühne's view is correct, the phenomenon finds a very ready explanation upon our hypothesis. It is necessary to assume that the retina is so constructed that the negative ions which are left in the bacillary layer by the departure of positive ions of the visual impulse, cannot penetrate into the inner strata of the retina, but can only move outward through the sclerotic. The presence of a structure of this sort is likely for several reasons, the most important of which, perhaps is the experimentally demonstrable fact that elec-

trical compensation does not exist between these layers. It is obvious that if such compensation did exist, the visual impulse would be destroyed almost as soon as it was generated. When we come to the study of simultaneous contrast we shall discover another reason why nature needed to establish a non-ionically permeable membrane between these regions. But in the injured retina this membrane is broken. Hence the positive ions of the visual impulse will be immediately followed by the negative ions left behind in the bacillary layer only for an instant. The result is a positive variation of the current of rest, straightway succeeded by a negative variation. Let us consider what should happen when the luminous stimulus which has been applied to the eye is suddenly removed. Upon extinction of the stimulus the ionization of the molecular resonators will abruptly drop. This means a sudden decrease in the number of positive ions moving centripetally in the retina to impinge upon the optic nerve fibres proper and to generate the ultimate visual impulse. Hence there will be a decrease in the positivity of the cut end of the optic nerve. There will also be a decrease in the impulse loss which has been feeding positive ions into the ocular media. This decrease will not immediately effect any marked change in the electrical condition of the media, on account of the relatively high concentration of the positive ions already present within them. A sudden fall in the supply of afferent ions will influence the optic impulse much quicker than it will the electrical status of the ocular media, and hence of the cornea. For this reason we should expect the removal of the stimulus to result in a second positive variation of the original current of
rest. This expectation is verified by experiment; the positivity of the cut surface of the optic nerve falls abruptly, so that it becomes relatively more negative with respect to the cornea, the potential difference existing under stimulation merely being augmented. This condition cannot be permanent, since the charge of the ocular media—and hence of the cornea—must also fall quite rapidly upon cessation of the high impulse loss which has been supplying them with positive ions. Hence the positive variation due to the withdrawal of the light is temporary, the current dropping very rapidly to that of rest. A fall under the current of rest may be explained by a decrease in the retinal concentration of the resonators, due to their augmented rate of destruction under the influence of the light.

1 Electrical Variations In One Eye Due to Stimulation of the Other....... *Engelmann and von Grijns* 2 have demonstrated the fact that stimulation of one eye is able to produce electrical changes in the other. This makes it necessary to assume that the two retinas are nervously connected. According to Quain 3 certain of the fibres of the optic nerve do not appear to be axons of the large perikarya of the "ganglionic" layer of the retina, but penetrate through the second and third layers to end in the inner synaptic stratum. The terminations are said to be frequently knobbed, resembling somewhat the terminations of the fibres of the rod-cells. It has been found by Parsons 4 that experimental lesions produced in one eye of a monkey are followed by the degeneration of certain fibres in the other eye. Quain tends to identify the free-ending fibres first mentioned with these inter-retinal nerves. It is therefore le-

1 W.H.R.R., p. 1051. 3 J.Q., p 228. 4 Journ. Physiol, 23. 2 GRIJNS, G. und ENGELMANN, TH. WILH.; Uber elektrische Vor-
gange im Auge bei reflektorischer und direkter Erregung des Gesichtsnerven; (1891); in Beiträge zur Psychologie und Physiologie der Sinnesorgane; S. 197-216. Hamburg u. Leipzig.
gitimate to suppose that any actual conduction of ions—in the manner already postulated—takes place from one retina to the other. In order to explain the phenomena of binocular contrast on the basis of such an interretinal conduction, it will be necessary to assume that the conduction in question involves a transfer of negative rather than positive ions. Apart from its introduction of a new element of complexity into our conception of the nerve impulse this assumption is not immediately objectionable.
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Definition of a Psycho-physical Threshold

A psycho-physical threshold may always be defined as the smallest physical quantity which, when a factor in stimulation, is capable of inducing a specified just perceptible psychical or sensory change. In the department of visual sensitivity, the physical quantity involved may be any one--or combination--of the following: (1) light intensity, $e$, (2) light wavelength, $\lambda$, (3) light purity, $P$, (4) the cross-section of the ray, or fascicle of rays involved (this may be called $a$), and (5) the time $t$ during which the light is acting. The minima considered may be expressed in absolute or difference measures, that is, the thresholds may be absolute or differential. The sensory changes to be studied in connection with stimulus changes in determining thresholds may obviously be changes in any one--or any combination--of the attributes of the elementary visual sensation, or in any characteristic of the visual image which is intimately related with the conditions limiting the elementary visual response.

The Conditions Cerebrally determining a Threshold Value.....

The mechanism which is undoubtably most closely connected with the determination of the specific character of thresholds is the cerebral mechanism paralleled by the conscious judgment of change and difference. In the case of visual response we may suppose this mechanism to be tuned in such a way that equal increments or decrements of that component of the visual cerebrosis intensity upon which judgment is to be passed always affect it in the same way, i.e., cause it to deliver a me-
chanical decision that a difference has been established. Since in the conscious subject sensation is never absent in any part of the visual field, the problem of a visual threshold is always a problem of the detection of differences or changes, and never of espying innovations. The physical nature of the cerebral discrimination mechanism is not difficult to imagine. Suppose that the visual sensory attribute, change of which is to be detected (with, say, the physical change of variation of the wave-length of the stimulating light), is redness. The cortical discrimination element, \( Z_{cd} \), is placed in communication with the R-element (cf. page 261), and comes into electrical equilibrium with it. The physical process of discrimination— or judgment of difference will consist in a change in the state of excitation of \( Z_{cd} \); this change in \( Z_{cd} \)'s excitation state setting off the series of motor activities which constituting "declaring the presence of a difference." Imagine, now, that the concentration of \( I_{r+} \) in the R-element increases; there will come a point at which the equilibrium state existing between \( Z_{or} \) and \( Z_{od} \) will be destroyed; things will occur in \( Z_{od} \) and the discrimination will be consummated. There is no reason for supposing that the difference required to upset the equilibrium in question will have anything to do with the absolute cerebral intensity of \( I_{r+} \), any more than the amount of water which falls over a dam per hour has anything to do with the depth of the river behind the dam; the work that can be obtained from the fall is determined simply by the difference in elevation which exists between the upper and lower water surfaces, to-gether with the rate of flow.
Suppose that the amount which any component of the cerebrosis concentration, \( c \), must be increased in order that a judgment of difference or change should be delivered is represented by the symbol \( \Delta c_s \), where \( s \) is any appropriate subscript. The quantity \( \Delta c_s \) merely constitutes the increase or decrease in concentration which must occur in order that the equilibrium existing between the cortical discrimination element and some element involved in the visual synergy should be upset. We shall assume that for any definite meaning of \( s \) this value \( \Delta c_s \) is constant. The factors influencing the threshold value of any factor in the stimulus will obviously be those factors of the visual response which intervene, quantitatively and qualitatively, between the stimulus and the cerebrosis. In order to bring about the change \( \Delta c_s \) it will be necessary to produce a certain alteration—to the extent, let us say, of \( \Delta t_s \)—of the elementary impulse intensity, since it is impossible that the action of the stimulus can be such as to directly alter the other factor involved in the cerebrosis intensity, viz., the cortical dissipation, \( \psi \). (cf. page 250). Let us denominate such quantities as \( \Delta c_s \) and \( \Delta t_s \), visual limena. Now the impulse limen, \( \Delta t_s \), must in its turn depend upon a retinal limen, which consists in an increase in the concentration of the visual ions in the rod or cone segments, due to an augmented rate of decomposition of the molecular resonators. The ultimate term in the limenal causation is thus \( \Delta m_s \) (cf. page 59); it is this term which must be realized under the influence of the stimulus limen or threshold. Now it will readily be seen that the relations: \( \Delta m_s = \Delta t_s = \Delta c_s \) cannot hold. In the first
place any increase in the impulse intensity, while it must result in an increase in the cerebrosis intensity, will also, on this very account, involve an augmentation of the cortical dissipation (cf. page 250), so that in order to accomplish a specified increase in the cerebrosis intensity a disproportionate increase (or decrease) in the impulse intensity will be required. In order that we may discover the relation which exists between the discrimination limen \( \Delta c_s \) and the stimulation limen, \( \Delta \hat{m}_s \), let us develop an expression for the generalized cerebrosis intensity, \( c \), in terms of the generalized stimulation \( \hat{m} \). When equilibrium is established in the visual response we may argue in terms of its quantitative attributes as follows. In our hypothesis, we have the following relations: (1) \( \phi = k_c c \), (2) \( \Sigma \gamma = k'_i \xi - \gamma \), (3) \( \zeta \gamma = k' \hat{m} \), and (4) \( i_+ = f^0(\hat{m}) \). (cf. pages 247 and 246) \( \zeta \gamma \) is the intensity of the visual impulse (elementary) at the retina, while \( i_+ \) is the retinal concentration of the visual ion \( I_+ \). From this assumption that the impulse intensity at the retina is proportional to the concentration of the visual ions (cf. page 246), it does not necessarily follow that the impulse intensity at this point is proportional to the rate of dissociation of the molecular resonators, \( \hat{M} \), since—considering the law of chemical mass action (cf. page 215) in connection with the reversibility of the resonance reaction—it is improbable that the ionic concentration—or ionization—in question is itself proportional to \( \hat{m} \). We have therefore indicated the relation existing between them by the function \( f^0 \), (4). Now under equilibrium conditions we have: \( k_c c = \phi = \xi = \phi \). But \( \xi = \zeta \gamma = k' \hat{m} \), \( \xi = k'_i \xi = \zeta \gamma = k'_i (k_c c) \). But, also, \( \zeta \gamma = k' \hat{m} \), \( \zeta \gamma = f^0(\hat{m}) \), from
which we may derive an expression for \( \dot{c}_c = k_1 f_0(\dot{m}) - k_1'(k_c c) \). Since, however, \( \dot{c}_c = k_c c \), we have: 
\[
k_c c = k_1 f_0(\dot{m}) - k_1'(k_c c),
\]
or
\[
k_c c(1 + k_1') = f_0(\dot{m}) = \frac{k_c}{k_1}(1 + k_1') c.
\]
Let us define \( k = \frac{k_c}{k_1}(1 + k_1') \). Then \( f_0(\dot{m}) = k c \), or--if \( f_0^{-1} \) represents the inverse of the function \( f_0 \)--: \( \dot{m} = k f_0^{-1}(c) \). Suppose, now, that we select a definite value of \( c \), viz., \( c_1 \); then we have \( \dot{m}_1 = k f_0^{-1}(c_1) \).

Let us now add to \( c_1 \) the discrimination limen, \( \Delta c \); the resulting increase (or, conceivably, decrease) in \( \dot{m} \) will represent the change which must occur in \( \dot{m} \) in order that discrimination should take place. Thus we have, for the stimulation limen:
\[
\Delta m = k \left[ f_0^{-1}(c_1 + \Delta c) - f_0^{-1}(c_1) \right]
\]
or, for a specific component of the response, \( s \), and for any value \( c \): 
\[
\Delta m_s = k_s \left[ f_0^{-1}(c_s + \Delta c_s) - f_0^{-1}(c_s) \right]
\]

It will be perceived that the stimulation limen is not necessarily constant with respect to changes in the value of \( c_s \). In discussing the hypothetical causes underlying Fechner's law for visual sensation, we shall consider this point in greater detail.

Evidently, even if we assume that changes occurring in the stimulus--and determining a threshold--are followed by strictly proportional changes in \( \Delta m_s \), the relation existing between the threshold value and the ultimate discrimination limen, \( \Delta c_s \), is by no means simple.

Thresholds of Light Intensity

When the physical quantity, the threshold value of which is to be determined, is the intensity, \( e \), of the stimulating light, the threshold will depend upon the light sensitivity, \( q_8 \) (\textit{cf.} page 213) of the resonator, \( M_8 \), and upon the other attributes of the light, which are
held constant. If \( q_s = \frac{\Delta \hat{m}_s}{\Delta e} \), we have, for a homogeneous light of definite wave-length: \( \Delta e = \frac{\Delta \hat{m}_s}{q_s} \), other things remaining equal.

If the stimulus attribute which varies is wave-length, the threshold is determined by the retinal limen function—that is, by \( \Delta \hat{m}_s \) —and by the resonance function, \( \hat{m}_s = f_{s\lambda}(\lambda) \), of the molecular resonator involved. Now we have defined the resonance gradient \( \rho_s \) as the first derivative of this latter function, and if we take the value of this derivative for a specific wave-length, \( \lambda_1 \), we may write: \( \rho_{s\lambda_1} = f'_{s\lambda}(\lambda_1) = (\delta \hat{m}_s/\delta \lambda)_1 \), from which we have:

\[
\Delta \lambda_1 = \Delta \hat{m}_s / \rho_{s\lambda_1}.
\]

It is obvious—or probable—that the value of the threshold of wave-length difference will change with the wave-length originally selected to vary. Thresholds of light purity—when heterogeneous light is employed as stimulus—obviously depend upon the same type of relationship. However when complementary ions are produced the discrimination function is complicated by the introduction of the complementation ion and its specific discrimination limen. The relationship is also modified algebraically on account of the complementation reaction. Only limited space (or time) prevents a consideration of this and other complex problems of visual thresholds. Of course—except in the stimulation of the retinal rods alone,—more than one component will be involved in almost any discrimination which can occur.

Absolute Thresholds.......... It may seem as if the above discussion applies only to difference, and not absolute thresholds. This is not the case, however, for in deter-
mining an absolute threshold, exactly the same factors are involved. Absolute and difference threshold experiments are separated only by the fact that in case of the former the value of \( c \) in the discrimination formula is not determined by the stimulus at all, but by the inherent forces of the visual mechanism. To the \( \Delta P \) (cf. page 60) values obtained we have added quantities perhaps quite incapable of influencing visual response in any way. On the other hand, we may hold unreservedly to the difference viewpoint if we choose to regard the physical limits of the visual spectrum as simple \( \Delta P \) values, which are very large, because the difference sensibility in the regions of the physical spectrum which are excluded from the visible spectrum is very small.

Thresholds of Extent of Retina Stimulated

It is obvious that if the fascicle of light rays falling upon any portion of the retina is cross-sectionally smaller than the retinal element (rod, cone, or system of rods or cones) upon which it impinges, the effect will be the same as if the intensity of the light were reduced, the fascicle being simultaneously thickened. The consummation of the cerebral change \( \Delta c \) depends ultimately only upon a definite change in the concentration of the visual ions in the retinal element with which it is connected. It makes no difference how light gets into this retinal element; the only important factor is how much enters in a certain time. The same number of light quanta (cf. page 152) entering as a very thin stream, will demolish a number of molecular resonators which would also be demolished if the light quanta were less densely aggregated. Perhaps this is not absolutely true for the
reason that a narrow path may become chemically exhausted with a quickness out of proportion with the time required—for the same number of light units—for the exhaustion of a broader path. When the retinal area stimulated is smaller than the cross-section of a retinal element, $Z_r$, the factor $a$ (the area of impact of the ray-fascicle at the bacillary layer) will enter into the light intensity threshold, so that we have: \[ \Delta m = k a e. \]

Experiment shows that the factor $a$ is of importance even when $a$ is as large as the area of the fovea. Our hypothesis permits a very simple explanation of this phenomenon. It is a well known geometrical principle that the ratio between a bounding line or surface and the area or volume which it envelope decreases as the area or the volume is augmented. Thus if $a$ is the area of a circle and $d$ is its diameter, the ratio $d/a = 2\pi r/\pi r^2 = 2/r$. Now in our hypothesis we have postulated a certain impulse loss which has a large value in the synaptic regions of the retina (cf. page 248); the larger the impulse loss, other things remaining equal, the larger must be the intensity of the stimulating light in order that the change $\Delta c$ should be consummated; this holds, of course, for a difference in intensity, as it does for the absolute intensity. We have supposed this impulse loss to be proportional to the impulse intensity at any point, and undoubtedly it is so proportional when an isolated responsive element is considered. But when an aggregation of contiguous elements is stimulated, a confining force—acting upon each element—is generated; this means an increase in $f$ (cf. page 248 ) for the region in question and thus a decrease in the impulse loss for a constant intensity. The nature of the process may

readily be perceived if we picture to ourselves the stimulation of retinal areas of various sizes. The total—not elementary—impulse loss in the synaptic regions corresponding with these stimulated areas will take place in two general directions, first radially, into the ocular media (cf. page 274), and second, tangentially, along the line of the synaptic strata themselves. The size of the stimulated area will not greatly affect the loss into the ocular media, but it must markedly influence the loss in a tangential direction. The total rate of impulse loss from the stimulated aggregate of retinal elements will depend upon the size of the surface through which that loss may take place. In order to find the effect produced upon each of the elements due to clumping—or in order to get the average effect—we must take the ratio between the bounding surface and the volume of retinal substance which is receiving the increased visual impulse. However, since the surface exposed in a radial direction is equal to the stimulated area, this may be left out of account, only the tangential surface being considered. The ratio of the charged volume to this surface is that of the area of a circle to its circumference: \( \frac{\pi r^2}{2\pi r} = \frac{r}{2} \). The average impulse loss from the co-excited visual conductors concerned will thus be proportional to 2/r, or inversely proportional to the radius of the stimulated area. This means that the elementary impulse intensities will be increased by a quantity which is directly proportional to \( r \). If this factor is large—as our studies upon the physical electrical phenomena of the eye tend to show—the effect will be approximately to make the impulse intensity proportional to \( r \) for small areas. In this event
the radius of the stimulating pencil of rays and the average intensity of these rays should be complementary with respect to the determination of a threshold. A result in harmony with this conclusion has been reached experimentally by Abney, who finds that "the smallest diameter, and not the area, is the determining factor." When the stimulated area is large (larger say than the fovea) the impulse loss in a tangential direction becomes negligible compared with that in a radial direction; hence for large areas the relation does not hold, the loss into the ocular media being proportional to the number of elements concerned, so that the average loss is constant in this direction. According to Rivers, "if a small field of coloured light is reduced in size till it appears colourless, it has been found that its colour may be restored, if other equally small areas are simultaneously illuminated with the same light." This effect receives very ready explanation upon our hypothesis. The disappearance of the color is due to the decrease of the concentration of the appropriate component of the visual impulse, particularly in the retinal synapses, below that necessary to an arousal of the discrimination reaction. Upon the stimulation of adjoining regions with lights having similar wave-lengths, more visual ions of the specific variety required are poured into the synaptic regions. Many of these go astray in these regions and enter that portion of the retina in which a feeble supply of the ions in question exists, but a supply which is just insufficient to consummate the appropriate $\Delta c$ in the cortical elements. The effect of the aberrant ions is obviously to bring up the concentration in this place so that (over)
it passes the liminal value.

The Cortex and Areal Thresholds............. of areal thresholds on the basis of impulse loss in the retina. It is obvious that they might also be explained by an application of similar methods of reasoning to the interaction of contiguous cortical elements. In the face of the great unity of the visual field we cannot deny that the parallel system of cortical elements possessed considerable unity of activity. It is presumable, not only that there will be a mutual reaction between the cortical elements via the agent of cortical dissipation, $\psi$, but that the excitation of one element may—at least in small groups—tend to augment that of immediately connected elements.

Importance of Retinal Concentrations of Molecular Resonators in Fixing Thresholds.... It is important not to forget that the specific concentration of each of the several molecular resonators in the retinal elements is directly related with the fixation of any threshold value depending upon the reaction of the resonator in question. The change of threshold values in the phenomenon commonly called adaptation, we shall hold to be due to change in the concentration of the molecular resonators. Other things remaining constant, a threshold (differential) will be proportional to the reciprocal of the retinal concentration with which it is involved.

The Psycho-physics of Thresholds........ Concerning the psycho-physics of visual thresholds, little need be said. It will be sufficient to point out that parallel with each $\Delta s_b$ there is a mathematically proportional $\Delta s_b$ (cf. page 115).

(over)

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Section XXX: An Explanation of Certain Temporal Relationships of Stimulus and Sensation.

Chapter 14: The Duration Threshold.

The Factors Influencing the Duration Threshold

At the beginning of the last Section (page 282), we mentioned the time, $t$, during which a stimulus acts upon the retina, as a physical factor capable of possessing a threshold value. We may speak of the least duration of any stimulus which can arouse the discrimination reaction as the duration threshold, $At$. The meaning of this threshold on our hypothesis is almost self-evident. In order that the cerebral modification $\Delta c$ should be realized, a certain definite change in the concentration of the visual ions in the retinal element must occur. This change can only be brought about by the absorption of a definite amount of radiant energy by the molecular resonators (cf. page 180). Now we have seen that this energy absorption, besides being influenced by the wave-length and intensity of the stimulating light, also depends, in the case of fascicles of rays smaller than the retinal elements themselves, upon the stimulated area. If the time during which any stimulus, no matter of what intensity or extensity, acts is made sufficiently short, this stimulus will bring about the dissociation of only a single extra molecular resonator; we may imagine that only three or four light quanta have time to enter the rod or cone before the light is cut off again; these may act destructively upon but one molecule; clearly in this case, given all intensity and extensity, the effect upon the ionization of the resonators will
be practically nil, and hence the discrimination reaction will not occur. As $t$ is increased there will come a point at which a number of resonators is broken down—in addition to the normal dissociation—just sufficient to consummate the cortical change $\Delta c$. This particular $t$ is $\Delta t$, the duration threshold for the particular light intensity, and light frequency, employed. Now it is obvious that the value $\Delta t$ will be correlated with the light intensity, in the compound threshold, in such a way that $\Delta m = k e \Delta t$, for the number of molecular resonators broken down depends merely upon the number of light units entering the retinal element; it does not depend at all (sic) upon how they enter; $n$ quanta per second for two seconds is equivalent to $2n$ quanta per second for one second; $\Delta m = k e a \Delta t$, when $a$ is smaller than the cross-section of the retinal element. In fact in order to determine the retinal effect, we have only to discover the dimensions of the whole column of light which passes through that element; the cross-section of this column is $a$, the length is $Ct$, where $C$ is the velocity of light, and $t$ is the time of action of the light. The volume of the column is thus $Cta$, and if we multiply this by the energy density, $e/C$, we have $tae$ as the amount of energy passing into the retinal element. The experiments of Charpentier, seem to show that for a threshold this product is a constant, and it may therefore be regarded as of fundamental significance in the study of the process of visual stimulation, and be given a special name: the energy threshold, $\Delta(\text{tae})$. When $a$ is greater than the cross-section of the retinal element which is being studied it must be replaced by unity, and under this condition the threshold begins

to be affected by the phenomena connected with impulse loss, which we have discussed in the preceding Section (page 286). The duration threshold is probably influenced by some factors other than those discussed above. Impulse loss, for example, must be largest at the very beginning of any increase in the impulse intensity; the energy of very brief visual impulses may be exhausted in raising the potential of synaptic spaces, no effect being evident in the cortex, while if the impulse had continued at the same intensity, an adequate cortical modification would have been produced on the basis of the synaptic charges built up in the first instance.

The Chemical Basis of the Energy Threshold........... The demonstrable existence of an energy threshold for visual stimulation is noteworthy verification of the hypothetical conception that makes this stimulation chemical in nature. The condition of affairs in the unstimulated cone segment—for example—may be compared to that which exists in a bowling alley that is in charge of an active pin boy. Light consists of a succession of little units of energy which knock down the molecules of the sensitive substance, much as the balls rolled by the bowlers upset the ten-pins. There are a very great many more molecules in the cone than there are pins in the alley and the aesthesogenases are much more active than the pin boy, but no doubt the process is very similar in character to that of the game of ten-pins; it probably contains an equal quota of the cosmic element of chance. But the point to be noted is that a definite amount of energy is required to knock a molecule to pieces, just as the upsetting of a ten-pin necessitates a definite ener-
gy. Other things being equal the number of equivalent elements of energy which enter the molecular field will determine the number of molecules destroyed, and--within certain limits--it seems to determine visual response.

Limits of the Duration Threshold..... The relationship which we have discussed above is evidently valid only for short durations. The intensity of visual response does not increase indefinitely with the time. The reason for this, upon our hypothesis, is obvious, for the existence of a duration threshold is dependent upon the fact that during short intervals visual ions are capable of piling up in the retinal elements, but our theory of the visual impulse compels us to admit that this accumulation of ions must finally be checked by the establishment of a new equilibrium between the convection of ions away along the neuro-fibrils and their production by photo-chemical dissociation.
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Chapter 15: The Rise and Fall of the Visual Cerebrosis.

The Nature of the Excitation-deexcitation Curve

The experimental studies of Exner and others have shown that when light of uniform intensity is thrown upon the retina, the resulting sensation change takes place in accordance with the curve shown in Fig. 3. The change is rapid at first but gradually decreases until a definite equilibrium condition is established. If the stimulus now be removed, the decline of the originally induced sensory modification will take place in accordance with a similar function of the time, except that the curve will be inverted, as shown in the figure, the fall being rapid at first, and finally much slower.

Explanation of the Form of the Curve

The question has been debated as to whether persistence and inertia of vision are of retinal or of cerebral origin. It seems likely that the phenomena in question depend upon the peculiarity of the visual processes taking place in both of these regions. In the preceding chapter we have discussed the principles underlying the so-called duration threshold effect, and we have seen that within certain limits the effect of light upon the retinal cells is cumulative, but that the nature of our conception of the visual impulse, and its dependency upon the concentration of visual ions in the retinal end-organs, force us to the conclusion that an equilibrium state must finally be produced. The genesis of this equilibrium state in accordance with our postulates must occur as a result of quantitative changes mathematically similar to those empirically observed, and above (over)
AN EMPIRICAL CURVE OBTAINED BY EXNER, SHOWING THE STATE OF
EXCITATION OF THE VISUAL APPARATUS AS
A FUNCTION OF THE TIME FOLLOWING THE
APPLICATION OF A STIMULUS............

Abscissae: Time elapsed since application of stimulus.


Exner's curve (A) is an excitation curve only. The curve of de-excitation (B) is interpolated from data by Fick.

See: TIGERSTEDT, ROBERT: A Text-book of Human Physiology, Trans. by J. R. Murlin; (1906); N. Y., pp. 540 and 539.
described. We have assumed that the intensity of the elementary visual impulse at the retina, \( \epsilon_r \), is proportional to the concentration of the appropriate visual ions in the retinal element: \( \epsilon_r = k_r \cdot i_+ \). Now let us suppose that at a time \( t = 0 \) when a definite light stimulus is applied to the retina, the concentration of these ions is \( i_{+1} \). Then, for this instant, we have: \( \epsilon_1 = k_r \cdot i_{+1} \). Since \( i_{+1} \) is a constant, we must have—neglecting for simplicity's sake, the reverse reaction (cf. page 215)—: \( \dot{m}_1 = \epsilon_1 \), the rate at which the visual ions are being produced is equal to the rate at which they are being carried away. But when light impinges upon the retinal element in question, \( \dot{m} \) will suddenly change, say to \( \dot{m}_q \); this means that an equilibrium condition no longer exists, that there will first be an increase in \( i_+ \), then an increase in \( \epsilon_r \), until finally we again obtain an equilibrium state, in which \( \epsilon_r = \dot{m}_q \). The impulse intensity at the retina at any time \( t \) during the establishment of this new equilibrium may be represented by the equation:

\[
\epsilon_r(t) = k_r \left( i_{+1} + \dot{m}_q - \int_0^t \epsilon_r \delta t \right).
\]

It will readily be perceived that up to a certain time, \( t_A \),—say—there will be a difference between the last two terms within the parenthesis, due to the fact that \( \epsilon_r \neq \dot{m}_q \), but that after this equality has been established, if we replace the integral \( \int_0^t \epsilon_r \delta t \) by \( \int_{t_A}^t \epsilon_r \delta t \) the two terms will be equal and opposite and hence will cancel, the difference: \( \dot{m}_q - \int_0^{t_A} \epsilon_r \delta t \) becoming part of a new concentration term, \( i_{+q} \). Inspection of the above function will show that when \( t \) is small \( \epsilon_r \) changes rapidly, but that as \( t \) increases the rate of increase of \( \epsilon_r \) becomes less and less until at \( t = t_A \).
it is zero. The graphical representation of the impulse intensity at the retina as a function of the time elapsed after sudden increase of the intensity of the stimulating light gives a curve which is identical in form with that empirically established for the rise of the sensory modification under such conditions. The curve in question—calculated on the basis of finite increments of time—is illustrated in Fig. 4. If after equilibrium is established, the luminous stimulus be suddenly removed so that $m$ sinks again to $m_1$, the rate of decrease of $r_t$ will be rapid at first, becoming slower with time, and approaching $r_1$ asymptotically. The curve of persistence of vision agrees with this result, which is illustrated in the accompanying Fig. 4.

Cerebrosis and the Time Function..... Thus we see that our fundamental postulates are in perfect harmony with the phenomena connected with the rise and fall of sensory modifications under the influence of sudden changes in the nature of the light stimulus. In the above discussion we have not, however, taken into consideration a fact of paramount importance, viz., the effect of increase in the rate of decomposition of the molecular resonators upon the reverse reaction—the deionization reaction—tending to reconstruct the resonators. The existence of this reaction makes it impossible that the effective rate of change of concentration of the visual ions in the retinal element should be equal—or even proportional—to $m$, for the initial increase in the ionic concentration resulting from an increase in $m$, means a consequent increase in the deionization reaction velocity, and hence a tendency to decrease the ionic con-

p. 305.
Fig. 4.

TO ILLUSTRATE THE CHARACTER OF THE EXCITATION-DEEXCITATION CURVE NECESSITATED BY OUR POSTULATES.

Abscissae: Units of Time Elapsed.

Ordinates: Impulse Intensity at the Retina: \( i_+ \).

A light stimulus of constant intensity was applied at 0 and removed at \( N \).

The above curve is a plot of the function: 
\[
\zeta_+ = t_m a - \sum_{0}^{N} \eta_+ t
\]
where \( t_m \) is the apparent rate of dissociation of the molecular resonator, is taken as a constant, 5, from \( t = 0 \) to \( t = N \), after which and before which it is zero. The function may be more conveniently written in the form:

\[
i_+ = 5t - \sum_{0}^{60} \frac{1}{8} i_+ t', \quad \frac{1}{8} \text{ being an arbitrary value for } k_r \text{ in } \zeta_r = k_r i_+ \text{, the variable } t \text{ becoming a constant } = N
\]
after this value is reached. The plot was made in the following way. During the first second the retinal concentration, \( i_+ \), was allowed a gain of 5 units. 1/8 of this was then subtracted and another gain of 5 units was added for the second second. The same process was repeated for 23 seconds, the curve representing the state of affairs at the beginning of each second before the decrement has been taken. At 23 seconds, the increments (of 5 units per second) were discontinued, and for each second thereafter a drop of 1/8th of the total concentration was permitted. Thus we have a qualitative representation of the manner in which the retinal excitation and de-excitation processes should occur in accordance with our postulates.

The above curve will be modified by the influence of the forces underlying Fechner's law (cf. page 317) if the intensity of the stimulating light is high. This modification, however, will not be qualitative. It should be noted that, in any case, the form of the excitation-de-excitation curve to be deduced from our postulates with reference to the laws of the visual cerebrosis is identical with the one figured above.
centration. As a result combined with the retino-neural effect above discussed there is a retino-chemical effect of an almost identical nature, tending towards the production of a similar type of function. In addition to the influences above mentioned there is a third which, in itself, is quite capable of accounting for the character of the curve of rise and fall of visual sensation changes. Our detailed explanation has been given in terms of the change of the impulse intensity at the retina. This is legitimate since upon our hypothesis, the impulse intensity at the cortex must follow the same general line of change as that at the retina. But it would be possible to dispense with the retinal process entirely—except as the source of a steady visual impulse—and to explain the phenomena of inertia and persistence of vision in terms of the cortical process alone. Inspection of the formula given on page 251 (top) for the cerebrosis intensity at any specified time will show that every detail of the argument presented above with respect to the course of the impulse intensity at the retina following a sudden increase in stimulation, will be paralleled in the analysis of the course of the cerebrosis intensity following a sudden change in the impulse intensity at the cortex.

Time to Rise to the Maximum and Intensity of Stimulus...

Exner has found that if the intensity, \( \text{e} \), of the light stimulus employed is increased in geometrical progression the time \( t_A \) required for the sensory process to reach a maximum decreases in arithmetic progression. Our theory makes this time roughly proportional to the reciprocal of the change in \( m \).

In discussing the retinal basis of Fechner's law for visual sensation (cf. page 312), we shall discover that \( \Delta m \), in general, changes in arithmetical progression when \( e \), the intensity of the light stimulus, change in approximate geometrical progression. Thus, when, as in Exner's experiments, the change suddenly produced is relatively large, we have: 

\[
\frac{\Delta}{m} = k \frac{1}{m} = k \frac{1}{\log e}, 
\]

approximately.  

The Talbot-Plateau Law and Flicker Sensation. 

A word may be said concerning the manner in which our hypothesis of visual response explains the well known proposition of Talbot, that when the retina is stimulated intermittently the "intensity" of the resulting sensation is the same that would result if an identical amount of light energy were employed in the same time in continuous stimulation. We have already made it obvious (page 295) that for short durations—less than \( \Delta \)—it is the energy alone which determines the extent of the modification produced at the retina or induced in the visual field. If this is true for a single short interval it must also be true for the sum of any number of such intervals. Flicker depends upon the alternate decrease and increase of the concentration of the visual ions in the retinal elements or in the elements of the visual cortex. The fact that our theory (cf. page 302) compels both of these elements to be considered provides a ready explanation for the fact that there are two types of flicker—the "fine" and the "coarse"—one of which disappears before the other, as the frequency of application of the columns of light energy is in-

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1 W.H.R.R., p. 1068.  
creased. The "coarse" flicker vanishes when the variations in cortical dissipation (cf. page 250) under the influence of the intermittent afferent impulse become so small as to have no effect upon the course of the cerebrosis; the "fine" flicker passes off either when stimulation is so rapid that the retinal concentration remains constant beyond the limits of responsiveness of the conducting system, or when the momentary cortical fluctuations are less than the discrimination limen, Δc. Upon our hypothesis we should expect the rate of stimulation necessary to complete fusion to vary with the intensity of the stimulus, since the more intense the retinal excitation the more intense will be the tendency towards centralward conduction, and the more intense the cerebrosis at any instant the more quickly will it fall from its maximum. In fact, we can very readily see that the frequency of intermittent stimulation required for fusion must be directly proportional to the intensity of the visual cerebrosis. For if we suppose that the disappearance of flicker depends, in the last analysis, upon the reduction of the fluctuations of the cerebrosis intensity below the discrimination limen, we may argue as follows. The cortical dissipation, \( \psi \), is proportional to the cerebrosis intensity at any instant: \( \psi = k_c c \). But \( \psi = -\Delta c/\Delta t \), so that the time which can elapse between one pulse of afferent visual ions and the next--dependent upon the frequency of stimulation--must be \( t_f = \Delta c/\psi \), if flicker is be exactly upon the verge of disappearance. Hence: \( t_f = \Delta c/k_c c \), and the stimulus frequency, \( \phi' = 1/t_f = k_c c/\Delta c = k_c \), the frequency requisite to just abolish flicker is proportional to the cerebrosis intensity. But the latter is proportional to the logarithm of the stimulus.
intensity, \( e \), so that we have, finally: \( \phi' = k \log e \), which is the result found by Grunbaum\(^1\). We must remember, of course, that the relation \( c = k \log e \) is only approximate. There are a number of interesting corollaries to the above consequences of our hypothesis with respect to intermittent stimulation which will explain certain deviations from the Talbot-Plateau law and certain peculiarities of flicker which we have not mentioned. Time forbids the development of these corollaries. We shall, however, have something further to say concerning the subject of flicker in discussing "flicker photometry" in connection with the problem of the luminosity of visual sensations. (cf. page 368).


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Section XXXI : The Explanation of Fechner's Law.

Fechner's Law and Its Interpretation in Terms of Our Hypothesis

Fechner's law states that the "intensity" of the sensation induced by any stimulus is proportional to the logarithm of the intensity of the stimulus. Reduced to our terminology this means that, in the case of visual response, the degree in which any one of the fundamental attributes of the elementary visual sensation (except B and complementation W) is exhibited, is proportional to the logarithm of the light intensity which is acting upon the corresponding molecular resonator.

Let us take the simplest instance, viz., the case presented by the aethromatic system, that involving only rod-cells in the retinal element. This system mediates the sensation attributes of W and B alone. Now in accordance with Fechner's law at any time when equilibrium exists in the visual system in question, we have: \( w = k \log e \), for any systemic element. From this we obtain, by use of the psycho-physical law (cf. page 113):

\( c_w = k \log e \), that is, the concentration of \( I_{W^+} \) ions in the cortical luminosity element (cf. page 260) is proportional to the intensity of the light acting in the retinal rod segment.

Fechner's Law is An Approximation......

Now Fechner's law is only approximately true for any department of sensory response, and in the case of visual sensation the approximation is rather rough. This—as we shall see—is what our hypothesis should lead us to expect, for there is no one simple process acting to maintain this general relationship between light intensity and the cerebrosis intensity, but—rather—a number of tendencies, all of which, however, are retinal in location. The
broadest statement that can be made of Fechner's law is to say that, in general, if the intensity of a stimulus is increased, the concomitant increase in the degree of the induced modification of the sensory field involved, is not proportional to the increase of the stimulus intensity, but, on the contrary, is a function of the reciprocal of the intensity; the degree of the modification fails radically to keep pace with the intensity of the stimulus. But it is by no means true that the relation between the two is strictly logarithmic, even within the limits of experimental error. This is shown in the accompanying diagram (Fig. 5) from Lloyd Morgan.

Our Hypothesis Lacks
The Mechanism Underlying Fechner's Law
Retinal..............

It will readily be perceived that our hypothesis of a cortical dissipation, \( \psi \), which is proportional to the given cortical concentration of cerebrosis intensity, \( c \), at any moment, and of an impulse loss, \( \eta \), which is similarly directly proportional to the impulse intensity, \( \iota \), makes it impossible to explain Fechner's law by an appeal to the cerebrosis or impulse processes in themselves, for when equilibrium obtains in the cortex, we have: \( \iota = \psi \eta = k_c c \); the cerebrosis intensity must, at equilibrium, always be proportional to the impulse intensity at the cortex. Similar relations hold between \( \iota \) and the retinal concentration, since at equilibrium: \( \iota = k_c c = \iota - k_i \iota_c \) (cf. page 247) = \( \iota - k_i \iota = (1 - k_i) \iota = k_r (1 - k_i) \iota \)

Fechner's law reduces in our hands to \( i = k \log \epsilon \), in connection with which remark it must be recalled that the function \( \log \) is only an approximation. In our discussion we shall usually deal with \( i = \) which must also be proportional to the (approx.) lo-
Fig. 5.

GRAPH SHOWING THE RELATION BETWEEN STIMULUS INTENSITY AND SENSATION INTENSITY CORRESPONDING.

Abscissae: Percentage of "White", "Red", or "Blue" Mixed With "Black" on a Rotating Disk.

Ordinates: Relative "Intensity" of the Induced Sensory Modification.

The black, red, and blue lines represent the relations for the admixture of white, red and blue respectively with black upon the rotating disk.

The dash line is a logarithmic curve calculated to the same scale.

From: MORGAN, C. LLOYD: The Relation of Stimulus to Sensation; (1900); Psychol. Rev., vol. 7, p. 231, etc.
Preliminary Glance at the Theoretical Chemistry of the Retinal Process.

Now there are several apparent reasons why the relation: \( i_+ = k_+ e \) cannot be true. We have assumed that \( i_+ \) depends upon the chemical decomposition (ionization) of a certain molecular resonator, \( \mathcal{M} \). Now let us suppose that the particular rod segment which we are studying is wholly unstimulated. Under these conditions the resonator in question will possess what we have called normal ionization (cf. page 217), and since equilibrium obtains, there will be a constant ionic concentration, \( i_{+1} \), and a corresponding impulse intensity at the retina: \( \zeta = \frac{k_+ i_{+1}}{r_{+1}} \).

Now the molecular resonator will be undergoing decomposition in the sense: \( \mathcal{M} \rightarrow I_+ + I_- \), at a definite rate: \( \dot{m}_1 \), but this rate will not equal \( \zeta_+ \), even at equilibrium, for the reason that a simultaneous reverse reaction: \( I_+ + I_- \rightarrow \mathcal{M} \) is occurring. If the rate of the resonance reaction is \( \dot{m}_1 = k_1 m \), and if the rate of the reverse--or deionization reaction--is \( \dot{m}_2 = k_2 i_+ i_- \), the apparent rate of decomposition of the resonator will be: \( \dot{m}_1 - \dot{m}_2 = \dot{m}_a = \zeta_+ = k_1 m - k_2 i_+ i_- \), the state of affairs through the visual system being that of equilibrium.

Now suppose that a light of intensity \( e \) be allowed to fall upon the rod or rod system which we are considering. The number of molecular resonators breaking down per second will increase in such a way that \( \dot{m}_1 = (k_1 + eq)m \), where \( q \) is the light sensitivity (cf. page 213) of the particular sort of resonator involved in the reaction, \( m \) being, of course, the concentration of the resonator in the rod. The apparent rate of decomposition thus increases to: \( \dot{m}_a = (k_1 + eq)m - k_2 i_+ i_- \).

Now with the help of this equation it may readily be perceived that \( \nu_n \) is not proportional to \( e \), but that as \( e \) increases, \( \nu_n \) will increase at a rate which is proportional to some reciprocal function of \( e \). This process will be ascribable to two principle causes, the most important of which is the fact that for every increase in the rate of the resonance reaction there will be an increase in the reverse reaction which is proportional to the second power of the first increase. This effect is due to the increase in the quantities \( i_+ \) and \( i_- \) corresponding with the augmentation of their rate of production. The second cause of the non-proportionality between \( \dot{n}_a \) and \( e \) is to be found in the decrease in the value of \( m \) which takes place with an increasing \( e \). These points will now be discussed in greater detail.

\[ \nu_n \text{ as the Square Root of } e \text{ .......} \]

Under equilibrium conditions the rate at which the visual ions are being produced in the retinal element must be equal to the rate at which they are being conducted or convected away, so that:

\[ \dot{\nu}_n = (k_1 + \text{eq})m - k_2 i_+ i_- = \nu_n = k_2 i_+ \text{.} \]

The rate of dissipation of the negative ions, \( \nu_1 \), must also be equal to their rate of manufacture, so that if the former rate is \( \rho = k_1 i_+ - \), we have:

\[ \dot{\nu}_n = \dot{n}_a = \nu_n = k_2 i_+ = k_1 i_- \text{.} \]

From the above we can obtain the relations:

\[ \nu_n = (k_1 + \text{eq})m - k_2 i_+ i_- = (k_1 + \text{eq})m - \frac{k_2}{k_r k_n} \nu_n^2 \text{, or if } k_x = \frac{k_2}{k_r k_n}, \nu_n = (k_1 + \text{eq})m - k_x \nu_n^2 \text{, from which: } \nu_n + \frac{1}{k_x} \nu_n = \]

\[ \frac{k_1 + \text{eq}}{k_x} m \text{.} \]

Solving this quadratic, we have:

\[ \nu_n = \sqrt{\frac{(k_1 + \text{eq})m}{k_x} + \frac{1}{4k_x}} m + \frac{1}{2k_x} - \frac{1}{2k_x} \]
If $k_x$ is large and $k_1$ small we have, approximately: $\zeta_\mathfrak{T} = k \sqrt{em}$, which means that as we increase $e$, $m$ remaining constant, $\zeta_\mathfrak{T}$ will increase only as the square root of $e$. If $e$ is unity, $\zeta_\mathfrak{T}$ will be $k$, but if $e$ increases to 100, $\zeta_\mathfrak{T}$ will only increase to $10k$, if $e$ becomes 10000, $\zeta_\mathfrak{T}$ will rise to 100, etc. It is obvious that this relationship is of the type of Fechner's law (cf. page 312). It is not necessary to assume that the constants present in the expression for $\zeta_\mathfrak{T}$ as obtained (page 316) are so proportioned as to be negligible in their effect upon the form of the curve. In the figure upon page 318 we have represented several curves depending upon functions similar to that derived for $\zeta$. The effect of constant terms outside of the radicle is merely to raise or depress the axis of the curve; terms within the radicle tend to flatten it, as shown (Fig. 6).

The Final Explanation of Fechner's Law in Terms of Our Hypothesis are not entirely consonant with the results obtained in the psycho-physical measurement of visual response. The curves in question approach an asymptote of proportionality between $\zeta_\mathfrak{T}$ and $e$; the actual experimental curves and the logarithmic curve do not do this, but come nearer approaching a constant ordinate as an asymptote. It happens that further analysis of the implications of our postulates will bring about the necessity of a final expression for the relation subsisting between $\zeta_\mathfrak{T}$ and $e$, which will be more in accord with the facts than a function of the type illustrated in Fig. 6. This final expression will result from a simple expansion of the equation already derived for $\zeta$, which will consist in an analysis of the term $m$. We have, in the above discussion, regarded
Fig. 6.

CURVES ILLUSTRATIVE OF THEORETICAL RESULTS WITH RESPECT TO THE HYPOTHETICAL BASIS OF FECHNER'S LAW.

Ordinates: $\eta_T = $ Impulse Intensity at the Retina.

Abscissae: $e = $ Light Intensity.

Curve A is a plot of the expression: $\eta_T = 6\sqrt{e}$

Curve B is a plot of the expression: $\eta_T = 6\sqrt{e} + 0.5$

Curve C is a plot of the expression: $\eta_T = 6\sqrt{e} + 10$

Curve D is a plot of the expression $\eta_T = 6\sqrt{e} + 40$
m as a constant, when, as a matter of fact, m is representable as a function of e, and hence must be a variable. When the apparent rate of change of the concentration of the molecular resonators in the retina--viewed from the side of the resonance reaction only--has a value greater than zero, it is clear that the value m--the concentration itself--must steadily decrease. If it does not, in point of fact, suffer a decrease, this must be explained by pointing out that the aesthesogenetic reaction $\overline{AB} + \overline{C} \rightarrow M$ (cf. page 219) is proceeding at such a velocity as to exactly counterbalance the effects of the destructive resonance reaction. In any equilibrium state the rate of the aesthesogenetic reaction and the resonance reaction must be equal.

From a qualitative standpoint, we may argue as follows to show that the concentration of $\overline{M}$ cannot remain constant under an increasing light intensity. With low values of $e$, $m$ will perhaps be practically constant, the aesthesogenetic reaction increasing in such a way as to maintain its normal point of equilibrium (cf. page 219). But as the rate of ionization of $\overline{M}$ grows very large--relatively speaking--the concentration of $\overline{M}$ ($m$) will begin to decrease, owing to the inability of the aesthesogenetic reaction to keep pace. We might in the first instance regard this inability as if it were purely dynamic in causation, but--from a more quantitative view-point--the nature and relations of this decrease may be easily demonstrated, as follows. The velocity of the aesthesogenetic reaction in the direction $\overline{AB} + \overline{C} \rightarrow M$ is determined by the relative concentrations, $\overline{ab}$, $\overline{c}$, and $m$, so that:

$$\dot{m}_a' = \dot{m}_3 - \dot{m}_4 = k_3 \overline{ab} \overline{c} - k_4 m.$$  

In order that the synthetic phase of the (aesthesogenetic) reaction should predominate over the
analytic one we must have either a decrease in \( m \) or an increase in \( \overline{ab} \) or \( \overline{c} \) or both \( \overline{ab} \) and \( \overline{c} \). The first change is brought about by the augmentation of the resonance reaction (cf. page 219), and it is only by virtue of the depressed state of \( m \) that the aesthesogenetic reaction can increase at all. At equilibrium we must have: \( \overline{m}_a = \overline{m}_a \), so that:

\[
k_3 \overline{ab} \overline{c} - k_4 m = (k_1 + \text{eq})m - k_2 i_1
\]

\[
eq (k_1 + \text{eq})m - k_x \frac{2}{r}
\]

(cf. page 316) =

\[
(k_1 + \text{eq})m - \frac{k_1 + \text{eq}}{k_x} m - \sqrt{\frac{k_1}{k_2} + \frac{k_2}{k_x}} m + \frac{1}{4k_x^2} - \frac{1}{2k_x^2}
\]

If we represent the radicle by \( f_1(\text{em}) \) we have:

\[
k_3 \overline{ab} \overline{c} - k_4 m = (k_1 + \text{eq})(1 - \frac{1}{k_x}) m - f_1(\text{em}) - \frac{1}{2k_x^2}
\]

\[
f_1(\text{em}) - k_4 m = (k_1 + \text{eq})(1 - \frac{1}{k_x}) m = -\frac{1}{2k_x^2} - k_3 \overline{ab} \overline{c}
\]

from which:

\[
m + \frac{f_1(\text{em})}{f_2(e)} = \frac{1}{2k_x^2} + \frac{k_3 \overline{ab} \overline{c}}{k_x + (k_1 + \text{eq})(1 - \frac{1}{k_x})}
\]

where \( f_2(e) \) equals the denominator of the right hand side of the equation. If we assume that \( f_1(\text{em}) \) is negligibly small compared with \( f_2(e) \), with \( m \), the above expression assumes the general form:

\[
m = \frac{k + k_3 \overline{ab} \overline{c}}{k + k_1}
\]

where in each case in which it is used \( k \) means---as usual---any constant. Inspection shows that if it were possible to resolve the radicle \( f_1(\text{em}) \) by any simple or complex means, the inclusion of the term \( f_1(\text{em})/f_2(e) \) in the equation would not alter its
general form. Regarding \( \bar{a} \) and \( \bar{c} \), for the time being, as constants, we have: \( m = \frac{k}{(k + ke)} \). Substituting in the equation
\[
\frac{\zeta}{k} = k \sqrt{em} \quad \text{(page 317)}
\]
we have:
\[
\frac{\zeta}{k} = \sqrt{ke/(k + ke)}
\]
k having a separate value in each case. The above type of function is entirely consonant with the facts of the psychophysics of visual sensation, as is shown in the accompanying Fig. 7 in which two functions of this type are plotted. When \( e \) is zero \( \frac{\zeta}{k} \) is zero, and as \( e \) increases a curve of a logarithmic character is traced out, \( \zeta \) approaching the ratio \( \sqrt{k/k} \) or a constant as \( e \) increases indefinitely. Since \( \frac{\zeta}{k} \) is not actually zero with zero stimulus—and also on account of the nature of our original expression (cf. page 316) the actual relationship is probably of the type: \( \frac{\zeta}{k} = k + \sqrt{ke/(k + ke)} \)
or:
\[
\frac{\zeta}{k} = k + \sqrt{(k + ke)/(k + ke)}
\]
k symbolizing, in each case, any appropriate constant, but the general form of the resulting curve will be the same. We shall speak of functions of the above type as stimulation functions, and the stimulation function of a particular molecular resonator, \( K_s \), we shall symbolize by the device: \( f_s(e) \). Since \( \frac{\zeta}{k} = k \frac{i}{i+} \), the relation: \( i_{s+} = k \frac{f_s(e)}{f_s(e)} \) holds good. We regard the above argument as a final, if not a maximally exact explanation of Fechner's law in terms of our hypothetical factors of the visual mechanism.

The Effect of Decreased Concentration of the Aestheseogens on Our Explanation of Fechner's Law

The above explanation of Fechner's law is valid even if it remains unchanged during stimulation. This could only be the
Fig. 7.

CURVES ILLUSTRATIVE OF THE FINAL EXPLANATION OF FECHNER'S LAW DEDUCED FROM OUR HYPOTHETICAL ASSUMPTIONS.

Ordinates: $\frac{\alpha}{r} = \text{Impulse Intensity at the Retina.}$

Abscissae: $e = \text{Light Intensity.}$

Curve A is a plot of the expression: $\frac{\alpha}{r} = \frac{6\sqrt{400e/(80 + 3e)}}{80}$

Curve B is a plot of the expression: $\frac{\alpha}{r} = \frac{6\sqrt{400e/(50 + 3e)}}{50}$
actual state of affairs if $\overline{ab}$ and $\overline{c}$ were very large or if the replenishment of these substrates went on at a rate proportional to the stimulation. Although the first possibility may be realized, the actuality of the second is doubtful. Whatever the case it is impossible to utilize the decrease in $\overline{ab}$ and $\overline{c}$ which must necessarily occur with long and intensive stimulation in the explanation of Fechner's law, since the effect of this decrease would only begin to be felt after the passage of some time, and the time does not enter into the law or its explanation. It is important, however, that the relationship expressed in the equation:

$$m = \frac{k + k \overline{ab} \overline{c}}{k + k_e}$$

be not forgotten, for it shows that the decrease in the concentration of the aesthesogens which must result from prolonged and especially from intensive stimulation will be reflected in the concentration of the molecular resonators for any intensity of stimulation and hence will bring about a reduction of the velocity of the resonance reaction under that intensity. We shall come back to this point in our discussion of adaptation and negative after-images. (cf. page 390).
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Section XXXII: Explanation of the Interrelations of Hue, Light, Intensity, and Wave-length.

Chapter 16: Why Hue is a Function of the Wave-length of the Stimulating Light.

A Detailed and Specific Explanation of the Empirical Relation: \( H = f(\Lambda) \)........

The primitive object of every hypothesis of visual sensitivity is an explanation of the functional relationship existing between the wave-length of the stimulating light and the hue of the sensation, when homogeneous or semi-homogeneous lights are employed. Most extant theories fail to provide an accurate and comprehensive presentation of the manner in which the hypotheses which they involve serve to explain this elementary fact of visual response. It is our purpose to develop the theory of the general relationship: \( H = f(\Lambda) \), which is established by experiment, in as rigid a manner as possible, making use of our fundamental hypothetical ideas. The hue, \( H \), of any elementary visual sensation, \( S \), may have not more than two component attributes, which we will designate as \( H' \) and \( H'' \), where \( H = H' + H'' \). \( H' \) and \( H'' \) may be any hues, except complementary ones.(cf. page 96). Arguing psycho-physically we have:

\[
h' = c_{h'} = \frac{h'_c}{k'_h} = \frac{(1 - k''_h'i'h'_r)}{k'h'_c} = \frac{(1 - k''_h'i')h'_r}{k'h'_c} = \frac{(1 - k''_h'i')f_{eh}(e)}{k'h'_c} \text{ (cf. page 321).}
\]

Now in our discussion of the hypothetical basis of Fechner's law, in the preceding Section, we have supposed the wave-length of the light the intensity of which varied—in the law—was itself constant. But if the wave-length is variant, the factor \( q \)—the light sensitivity of the resonator involved—cannot be constant, so that the
expression for the apparent rate of decomposition of the resonator, \( M_h \), under the action of a light \( L_{x\alpha} \), must be:

\[
\dot{m}_a = (k_1 + e \cdot f_{h\lambda}(\lambda) )m - k_2 i^1
\]

where \( f_{h\lambda}(\lambda) \) is the resonance function of the resonator in question (cf. page 287). If the above relation be employed as the basis of a line of mathematical reasoning entirely analogous with that followed in the preceding Section, it will appear that in what may be called a complete stimulation function, both the light intensity and the wave-length will be present. If we symbolize functions of this sort by the terminology: \( \lambda = f_{\lambda\alpha\beta}(e, \lambda) \)
we can write:

\[
h' = \frac{(1 - k_{h\lambda1}) f_{\lambda\alpha\beta}(e, \lambda)}{k_h'c}
\]

The hue \( H' \) will obviously depend upon the wave-length for its sensory degree, \( h'' \), in an entirely analogous fashion, so that:

\[
h'' = \frac{(1 - k_{h''1}) f_{\lambda\alpha\beta}(e, \lambda)}{k_h''c}
\]

But if both \( H' \) and \( H'' \) are thus functions of the wave-length, the total hue, \( H \), must also be determined by the wave-length.

Nature of the Complete Stimulation Function. The exact nature of the complete stimulation function spoken of above may readily be made clear. If the original resonance function is defined in such a way that, the actual rate of dissociation of the resonator (cf. page 315), \( \dot{m}_1 = [k_1 + e \cdot f_{x\alpha}(\lambda)]m \), it is evident that \( f_{x\alpha}(\lambda) \) may be substituted for \( e \) in all of the expressions of the preceding Section, and that if \( e \) is not constant we have:

\[
\lambda = f_{\lambda\alpha}[e \cdot f_{x\alpha}(\lambda)] = f_{\lambda\alpha\beta}(e, \lambda), \quad \text{the complete stimulation function.}
\]
Chapter 17: The Exact Properties of the Molecular Resonators.

The Problem

In Section XXVI we have postulated the existence in the cone segments of the retinal bacillary layer of four specific molecular resonators, and in the rod segments of a fifth. In that Section we have also pointed out that each of these resonators must finally be assigned definite quantitative properties. It is to the problem of the specification of these properties that we now turn (cf. page 268).

The Effect of Fechner's Law Upon Our Determination of Resonance Functions

Perhaps the most fundamental mathematical characteristic of the specific molecular resonator is its resonance function. This we have defined (on page 214) as the mathematical relationship existing between the rate of dissociation of the resonators and the wave-length of the stimulating light. Now on account of the fact that the impulse intensity at the retina is not proportional to the actual dissociation rate but, as our interpretation of Fechner's law reveals, is proportional to the apparent dissociation rate, the resonance function of a particular resonator will not be represented in the corresponding function giving \( \Theta \) in terms of the light wave-length. We have seen in the preceding chapter (page 326) that the resonance function is related with \( \Theta \) in just the same way that the light intensity, \( e \), is related with it. Hold \( e \) constant, and the resonance function can be substituted in the place of \( e \), thus: \( \Theta = f \Theta \left[ f \Theta \left( \frac{\lambda}{\lambda} \right) \right] \). This means that the effective resonance gradient, \( \delta \Theta / \delta \lambda \), will decrease numerically with increasing reso-
nance, if the actual gradient remains constant; in other words, the curve representing the effective resonance function will be flattened towards its summit. Its general sense—the position of the maximum, etc.—will, however, coincide with that of the curve for the actual resonance function. It follows from the above that the effective resonance curves of the same resonator at different intensities of stimulation will be different; at high intensities, the curves will be approximately flat while the lower the value of \( e \) the greater will be the average value of the effective resonance gradient. We shall later employ this result in the explanation of several peculiarities of visual response (cf. page 337).

The Resonance Functions.... In Fig. 8 we have illustrated the typical form of the relation between the intensity of response of a resonator and the wave length or frequency of the stimulus applied to it. Each one of the five molecular resonators, \( M_r \), \( M_g \), \( M_y \), \( M_b \), and \( M_w \), must possess a natural function of this sort. The time allotted for the completion of this thesis is insufficient to permit a discussion of the reasons which lead us to adopt curves having the general form shown in Fig. 9. The functions there represented are to be regarded as actual resonance functions, and it must be recalled that these are connected with effective resonance only in the way above indicated. The expression for the actual rate of dissociation of the molecular resonators under the influence of a light, \( L_\lambda \), was \( \dot{m} = (k_1 + eq f_\lambda) m \). Each of the resonance curves of Fig. 9 may be regarded as a plot of the above function in which \( em \) is regarded as a constant quantity. The curves are not to
Fig. 9.

**GENERAL CHARACTER OF A RESONANCE FUNCTION GRAPHICALLY REPRESENTED....**

Ordinates: Relative Intensity of Resonance.

Abscissae: Wave-lengths.

$\bar{n}$ is the wave-length corresponding with the natural frequency of the resonator.

See: LAMB, HORACE: The Dynamical Theory of Sound; (1910); Lond., p. 33.
FIG. 9.

Graphical representation of the approximate nature of the resonance functions of $M_r, M_y, M_g, M_b$, and $M_w$. 

MOLECULES DECOMPOSED PER SECOND PER UNIT LIGHT INTENSITY.

Relative Number Concentration.
Fig. 10.

SHOWING THE FLATTENING OF THE RESONANCE FUNCTION CURVE OF Fig. 8 DUE TO THE PFECHNER'S LAW CURVE OF Fig. 7.
be looked upon as rigidly quantitative in character, however, and the writer considers them quite tentative, believing that a profounder knowledge of the requirements to be met would in all probability necessitate definite changes in the form and position of the several resonance functions symbolized.

The curves in Fig. 9 are intended to give a rough idea of the relative light sensitivities of the several molecular resonators. Kunkel finds that the period required for the visual sensation to rise to a maximum after sudden application of a stimulus is least in case light of long wave-length is employed. The fact that there is no photo-chromatic interval for red, and that red is one of the last hues to disappear with decreasing light intensity, also indicate that $M_r$ has the greatest light sensitivity. Similar data have been used in settling upon the relative heights for the curves for $M_y$, $M_g$, and $M_b$. It goes without saying that the resonator $M_w$, the visual purple, possesses a high value for $q$. The curves as given represent resonance with respect to light of unit intensity, -- assuming also, the several concentrations, $m_r$, $m_g$, etc., to be unitary. Both $Y$ and $B$ disappear quickly upon lowering the light intensity, and last longest when the intensity is indefinitely increased; each of these properties speaks for low light sensitivity.

The Retinal Concentrations of the Resonators...... It will be perceived that the retinal concentrations, $m_r$, $m_y$, etc., of the respective resonators occupy a position mathematically similar to that filled by the light sensitivity; any decrease in these concentrations means a decrease in the effec-
tive sensitivity of the retinal element concerned to lights of wave-length corresponding with the natural period of the resonator affected. These concentrations are evidently variable (cf. page 323); it is possible that we shall have occasion to specify their normal relative values at a later point in our discussion.
Chapter 18 : An Explanation of Complementation and Some of its Corollaries.

The Mechanism of Simple Complementation... A glance at Fig. 9 will show that if a light of \( \lambda = 650 \) (say) be applied to a retinal cone it will bring about a perceptible increase in the ionization of all four molecular resonators there present, but that there will be a special increase in the dissociation of \( M_x, M_y \) and \( M_z^e \), the greatest increment being, obviously, that occurring in \( M^e_x \). From this it may at first be thought that there will be a concomitant augmentation of the three components of the impulse intensity, \( \xi_r, \xi_y \) and \( \xi_g \), resulting finally in a rise of the cerebrosis intensities: \( c_r, c_y \) and \( c_g \).

Further reflection, however, will make it clear that, upon our hypotheses, only the first two increments, \( c_r \) and \( c_y \), can actually take place, since as the retinal impulse passes through the ganglion cells of the inner retinal layer all of the \( I_g + \) ions will necessarily be removed by the reaction which there occurs between the complementation substance (cf. page 270) and the components of the impulse. With an excess of \( I_r + \) ions in the impulse it will be impossible for any \( I_g + \) ions to pass through the ganglion cells. However, for every pair of these two ions removed by the complementation reaction, an \( I_x^{++} \) ion will be added. Now suppose that to the original stimulus we add a light of \( \lambda = 490 \), the intensity of which is so chosen that, as a result of the double stimulation we have: \( \xi_r = \xi_g = \xi_{rb} \), and \( \xi_y = \xi_{rb} \), the four impulse intensity components at the retina being represented. In this case none of the ions originating in the cone will reach the cortical element, but all will be removed in
the complementation reaction, the number of $I_{w}^+$ equivalents (cf. page 272) added being $2'_{Tr} + 2'_{Ty}$, in terms of impulse intensity at the retina (neglecting, for simplicity's sake the impulse loss). The consequence will be that the only cortical element responding will be the luminosity element (cf. page 260), and the induced sensation will be characterized by the fundamental attributes, W, and B, only. This, in brief, is our description of the mechanism underlying complementation; complementary lights are merely those so chosen that when both are applied to a retinal cone element the resulting complementary impulse intensity components (at the ganglion cells) are severally equal. The position of complementary lights in the spectrum is determined by the retinal and neural conditions underlying and limiting this result.

Explanation of "Color-Mixture" If two lights are thus chosen which are not complementary in toto, but are of such a character as to stimulate the production of certain complementary ions at a rather high velocity, the result will obviously be the induction of a sensation differing in hue from that which would have been induced by either of the lights separately, and less saturated than either of these sensations, that is—to stick to our own terminology—it will have a relatively low chroma, h, as compared with a sensation of identical hue, induced by a homogeneous light. Suppose, for example, that we stimulate the same cone with lights of $\lambda = 650$ and $\lambda = 550$. Both of these lights will act to increase $'_{Ty}$; the first, however, will augment $'_{Tr}$ while the second will augment $'_{Tg}$. Suppose that the e values of the two lights are so adjusted that $'_{Tg} = '_{Tr}$. Then, in the complementation reaction, both of the ions represent-
ed will be completely removed, only the $I_{y^+}$ ions remaining. The induced sensation will thus be one of relatively low $h$, characterized by the fundamental attributes $W$ and $Y$. In the language of common sense "we mix red and green and get yellow." An entirely analogous line of reasoning may be developed with reference to any heterogeneous light stimulus, and if we had the time, we could derive—from our fundamental postulates—quantitative expressions for the results of the mixture of any set of lights.

Explanation of the Chroma Relations of Different Heterogeneous Lights... J. J. Müller, and more recently von Kries, found that when a heterogeneous light stimulus is made up of two (or more) lights having wave-lengths falling between the limits $\lambda = 760$ to 567, or $\lambda = 390$ to 492 the chroma of the induced sensation does not differ from that of a sensation induced by a homogeneous wave yielding the same hue. The reason for this may very readily be perceived in the diagram (Fig. 9), for there it will be seen that within the regions specified the proportion of complementary ions generated by lights of varying wave-length is practically constant. It is only with the rise of $M_g$ on the one hand and of $M_y$ on the other, that noticeable complementation begins to ensue. (cf. also Fig. 14, p. 367)

The Heterogeneous Complementary of Green... No homogeneous light is capable of inducing a hue which shall be complementary with respect to green; the complementary of $G$ is purple ($R + B$). The reason for this striking fact may be gathered from our figure, in which it appears that a light capable of exciting $M_g$ to a maximum also excites $M_y$ very strongly. As a consequence, both $I_{y^+}$ and $I_{b^+}$ are demanded for complementa-
tion. It is the presence of this same apparently adventitious excitation between \( \lambda = 625 \) and \( \lambda = 725 \) that makes it necessary to move so far towards the short wave-length end of the spectrum to find the complementary of light from this region; the introduction of a large \( I_\beta \) component is requisite.

Points of Least Chroma

Of all the sensations induced by homogeneous lights those characterized by the hues \( Y \) and \( B \) are least in chroma. Our diagram provides a ready explanation for this fact, for the production of complementary ions under varying stimulation with pure lights shows two maxima, one at \( \lambda = 575 \) (approx.) and the other at \( \lambda = 500 \). (cf. Fig. 14, page 367.)

The Disappearance of Hue

With Increasing Light Intensity

When the intensity of any homogeneous light is indefinitely increased the induced sensation increases in luminosity and decreases in chroma until finally it loses hue entirely. This phenomenon we may explain in terms of our theory as follows. Every light stimulus acts upon every molecular resonator. At low intensities a light of wave-length \( \lambda = 655 \) (say) acts very strongly upon \( M_\lambda \) and only weakly upon \( M_g, M_y \) and \( M_b \). But as the intensity is increased the increase in the several components of \( \xi \) follows Fechner's law—as we have interpreted it—(cf. page 322) and for this reason each of these components approaches a definite maximum; the nearer any component is to the maximum natural to it, the less will any change in the light intensity affect it. The result is that, no matter what the wave-length of a light may be, its effect upon the several resonators at very high intensities is the same.
If we suppose that the constants determining the maxima in question are of such a character that, when the maxima are attained the rate of effective disintegration of the resonators are such as to produce complementary ions in balanced numbers, it follows that with high intensities of light stimulation, the fundamental attribute of the induced sensation will be W only, no matter what frequency may characterize the light. Another way of expressing the facts--or hypotheses--is to point out (cf. page 328) that at high intensities the curves representing the effective resonance functions are so flattened as to be practically straight lines. The fact that Y and B disappear later than R and G with increasing e shows that the resonators, \( M_y \) and \( M_b \), have lower light sensitivities, \( q_y \) and \( q_b \), than have the resonators \( M_r \) and \( M_g \), so that as e advances, \( \alpha_y \) and \( \alpha_b \) do not so quickly enter the "flat" regions of their respective stimulation function curves (cf. page 332 and Fig. 91). In the course of the change above described, the sensory hues themselves alter--in addition to the diminution of chroma and increase in luminosity--the fundamental hue, Y, tending to predominate. \(^1\) The reason for this predominance may be found in our hypotheses. We have noted the presence of a strong \( \hat{m}_y \) excitation along with both \( \hat{m}_r \) and \( \hat{m}_g \); if wavelengths corresponding with the maxima of either one of these latter quantities be employed, and the value of e be indefinitely increased, the relatively high light sensitivity of \( M_r \) and \( M_y \) will cause their two excitations to straightway blot each other out in accordance with the principle above set forth, while, owing to the relatively low light sensitivity of \( M_y \) and \( M_b \), the effective dissociation rates of these last two resonators will re-

\(^1\) Rood, O.N.: Modern Chromatics; (1875); N. Y. p. 181.
main—for some time—non-complementary in their ratio. Experiment shows that as e is increased G first passes into YG, then into YW and finally into W; R becomes orange, then WY.1

The Case of Violet...... Examination of our diagram will elucidate the manner in which we have sought to explain the very peculiar fact that the shortest light-waves capable of inducing visual sensation repeat the fundamental attribute, R, which is also, more strongly, induced by the longest light-waves. We have supposed that the high light sensitivity of $M_R$ causes it to resonate appreciably with lights of all wave-lengths. Between $\lambda = 575$ and $\lambda = 480$, however, this resonance can have no chromatic effect in the cortex, on account of the presence of an excess excitation of $M_G$; when $\frac{E_G}{E_R}$ is greater than $\frac{E_R}{E_R}$, no $I_R+$ ions can pass through the retinal ganglion cells. The only cortical effect will be an enfeeblement of the chromatic components of the cerebrosis, so that the parallel sensation will have a relatively low chroma. This effect is well recognized. At $\lambda = 480$, $\frac{E_G}{E_R}$ and $\frac{E_R}{E_R}$ become equal, so that only the $I_R^B$ component of the impulse is chromatically effective. The $M_G$ excitation, however, falls more rapidly than the $M_R$ excitation—as our original assumptions should lead us to expect—so that at about $\lambda = 435$, the discrimination limen, $\Delta c_R$ (cf. page 284) is surpassed by the increasing effective $\frac{E_R}{E_R}$, and the visible spectrum thus ends with a blue faintly tinged with red, viz., violet. This interpretation of the sensory hue, violet, is borne out by a number of facts, important among which are the following. If a light of about $\lambda = 400$ is employed as a stimulus, with decreasing e, the sensory hue approaches purple, i.e., relatively less B

1 ROOD: loc. cit.
and more R being exhibited. This is exactly what should be expected if—as we have assumed—M₀ has a lower light sensitivity than Mᵣ. With very high light intensity violet changes to pure E₁, this, again, is to be expected in accordance with our postulates, since at high e the activities of Mₑ and Mᵣ quickly cancel each other—through the complementation reaction—for light of any wave-length (cf. page 337). Other facts in favor of the above explanation of the very remarkable psycho-physical relationships of the sensory hue, violet, will be considered in our discussion of visual adaptation and fatigue. A word may be said in criticism of current hypotheses with reference to their treatment of the psycho-physics of violet. Hering's hypothesis accounts for the facts quite satisfactorily upon the assumption that with lights of very short wave-length the "red-green substance" (cf. page 128) undergoes a second "dissimilation."

All of the other theorists, however, either neglect the problem entirely or pass over it with a remark rather than an explanation. To the present writer it appears that the failure of an hypothesis to take into account this peculiar repetition of the attribute R at the short wave-length end of the physical and visible spectra, amounts to entire insufficiency, --if the hypothesis in question be judged from the physical realistic point of view, an attitude we have taken much pains to defend (cf. page 43 ff.)

1 ROOD: loc. cit.


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6. TSHERMAK, A.: Übe die Bedeutung der Lichtstärke und des Zustandes des Sehorganes für farblose optische Gleich- ungen; (1898); Pflüger's Arch., Bd. 70, S. 297.

7. --: Über das Verhältnis von Gegenfarbe, Kompensa- tionsfarbe und Kontrastfarbe; (1907); Pflüger's Arch., Bd. 117, S. 473.

The Limits of the Spectrum. A glance at our graph of the several resonance functions (Fig. 9, page 330) will show that it provides no adequate explanation for the fact that the visible spectrum comes to an end at about \( \lambda = 760 \) in normal visual response. Although at the short wave-length end of the spectrum the curves come nearer the zero axis there is still a difficulty in reconciling their form with the sudden drop in sensation quality which occurs at this point. There are two ways in which we may account for the abrupt truncation of the resonance functions at \( \lambda = 760 \) and \( \lambda = 390 \). In drawing the curves in Fig. 9 we have adhered very closely to the form of the symmetrical resonance function given in Fig. 8. Now as a matter of fact curves representing chemical change with respect to different light frequencies are not of this absolutely symmetrical type; they are generally roughly symmetrical, but—as illustrated in the accompanying Fig. 11 may often exhibit a considerable skew, and while on one side they may approach the axis gradually on the other they may drop very abruptly. From the standpoint of empirical chemical results we may legitimately alter our resonance function curves in such a way as to harmonize with the facts concerning the limits of the spectrum. However, there is another mode of explaining the facts in question which—if defensible—is to be preferred. It is well known that the ultra violet light is powerfully absorbed by the ocular media; this absorption has been shown to begin at about \( \lambda = 390 \). On the other there seems to be no evidence that—when examined in vitro the
Fig. 11.

SHOWING THE ACTION OF LIGHT UPON THE SALTS OF SILVER UNDER VARIOUS CONDITIONS.....

Abscissae: Wave-Lengths of Light.

Ordinates: Extent of Chemical Change, Relative.

From the Encyclopaedia Britannica, article: Photography, 11th ed., vol. 21, p. 496, Fig. 1.
media of the eye possess any special absorptive power for the lights lying between $\lambda = 760$ and $\lambda = 1400$. Unless, therefore, it should appear that the absorption phenomena are different in the living and active than in the enucleated eye, it will be necessary to have recourse to the first explanation, suggested above, of the position of the spectrum end in the red. In connection with this discussion our consideration of the fundamental principles of thresholds of every character (page 287 ) should not be forgotten.

All of the Resonators are at Least Slightly Excited by every Visible Light.... There has been consider-able discussion, particularly among adherents to the Young-Helmholtz hypothesis, as to whether all of the visual sensitive components, as $M_r$, etc., are affected, to some degree, at least, by lights of all wave-lengths corresponding with the visible spectrum. In our hypothesis all five resonators, $M_r$, $M_y$, $M_g$, $M_b$, and $M_w$, are acted upon to a certain extent by all lights of wave-length between $\lambda = 760$ and $\lambda = 390$. They are also slightly affected—probably only subliminally—by lights lying outside of these limits. Now the curves obtained by König and Disterici to represent the fundamental physiological sensibilities of visual response, and which are accepted as the most satisfactory descriptions of the elements of the Young-Helmholtz hypothesis now extant, were constructed upon the assumption that the visible spectrum could be legitimately divided into three (or five) distinct regions; in the mid region the excitation $M_g$ was effective, but in the two outer regions its effects were supposed to be entirely absent. According to our point of view this assumption (over)
1 W.H.R.R., p. 1054.

2 KONIG, A., und Dieterici, C.: Zeits., ibid., (1893); Bd. 4, S. 283.
is quite unjustifiable. In addition to the facts cited on page 335 above to show that there is a strong Y component in the farthest spectral red, as well as in the spectral green, we may mention the following phenomena which point in the same direction. When a spectrum is viewed in the periphery of the visual field and the energy of the stimulus is increased, all of the hues except B receive an added yellowness, \( \delta y \); with decrease in the intensity of the physical spectrum a decrement, \(-\delta y\), or an increment of b, \( \delta b \), occurs in all of the hues except Y itself. With respect to change in light intensity, there are thus only two constant spectral hues, Y and B. This fact is readily explicable upon the basis of our hypothesis, but receives no explanation at all from König and Dieterici's curves. \( M_B \) is undoubtedly the oldest and the least sensitive of the chromatic molecular resonators; with increasing light intensity the hues R and G are blotted out by the Fechner's law complementation effect described above (page 337), and since the \( m_Y \) excitation keeps ahead of \( m_B \) the result is an addition of Y; with decreasing intensity the converse effect takes place, relatively more B being included. When the visible spectrum is seen (fragmentarily) at the fixation point continued fall in the light intensity is accompanied by an increased redness of all of the spectral hues, except, of course, the green. The reason for this is obvious, since the \( m_R \) excitation is the last to fall below the threshold (cf. Fig. 9). This phenomenon is obscured in the peripheral field by the rise of the \( m_W \) excitation with dark adaptation.

In discussing retinal fatigue we shall point out some other facts

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1 NICATI, W.: La Psychologie Naturelle; (1898); Paris. pp. 63-65.
which very strikingly confirm the conception of a universal—if differential—excitability of all of the resonators. Burch has noted the fact that at low intensities the sodium (Fraunhofer D) line often appears distinctly green. Examination of our figure will show that a slight relative fatigue (lowered \( m_r \)) of the resonator \( m_r \) would suffice to give the \( m_g \) excitation the ascendency in this spectral region at low intensities, when the small value of \( q_y \) permits the \( m_y \) excitation to fall below the threshold. Burch has also noticed that when the attention is directed to the spectral colors their hues appear to oscillate. For example, if the attention is concentrated upon the orange, "in a couple of minutes it will flicker and change, appearing R and G by turns." This phenomenon may readily be explained in terms of variations in the sensitivities of the cortical chromatic elements—due to the attention process—if we assume, as our postulates do assume, that in the orange, both \( m_r \) and \( m_g \)—as well as \( m_y \)—are strongly present. Of course, a certain degree of retinal fatigue will also be requisite to account for the alternation of complementaries, but Burch remarks that in examining sodium light in this way, the effect only appears when the eye is obviously fatigued. The same observer has seen a similar flickering in the spectral blue-green, first B and then G being dominant, and in the indigo there is a flicker between B and violet. All of these facts are readily explicable in terms of our diagram.

Effect of Daylight....... A word may be said concerning the theoretical aspect to stimulation of the retina with daylight. If we define daylight as a collection of lights

1 BURCH, G. J.: An Experiment in Colour Sensation; (1897); Journ. of Physiol., vol. 21, p. xxvii.
of (practically) all wave-lengths, it will be perceived that every component will act upon every resonator in such a way that the resulting effect will be the same as if a homogeneous light of very high intensity were employed. For example, considering the case of the resonator \( M_r \), stimulation with daylight will bring about a rate of dissociation of this resonator proportional to the entire area enclosed by the curve given for \( M_r \) in Fig. 9. To bring about an equivalent rate by the use of a homogeneous light a very high intensity would be required. Light homogeneity is, of course, always a relative thing; an absolutely homogeneous light may very well be conceived, but when we depend for its selection upon the spectroscopic analysis of daylight, we find it impossible to obtain a pencil of absolutely pure rays which shall possess a finite energy. We are therefore forced to use lights varying in wave-length between narrow limits. Suppose these limits to be determined by a wave-length difference, \( \delta \lambda \); then if the energy of the light per unit \( \lambda \) is \( \bar{e} \), we have for the intensity of a pencil of light of standard dimensions \( \epsilon = \bar{e} \delta \lambda \). From this: \( \bar{m} = \bar{e} q \int f_{\lambda}(\lambda) \delta \lambda \). But for daylight we have: \( \bar{m} = \bar{e} q \int f_{\lambda}(\lambda) \delta \lambda \). It is seen, therefore, that the effect of daylight will be a tendency to bring the excitation of all of the molecular resonators up to the Fechner's law complementation point, so that all of the hues will vanish from sensation. Since the resonator, \( M_r \), is the most light sensitive, we should expect the addition of daylight to a homogeneous light of any wave-length to result in a relatively excessive increase in \( M_r \), so that the corresponding hue will gain—or tend to gain—in redness. This is found to be the case, by Brücke. Rood, on the other hand, finds
that an effective addition of violet occurs. This result may possibly be explained by the presence of an excessive proportion of "blue" in the light employed by this worker; small disproportionalities, however, should have no effect upon the result when the complementation point is reached, as, of course, it is not, in the experiments in question. With relatively large amounts of daylight the resonators $M_r$ and $M_g$ may be conceived to approach this point, after which addition of more daylight should result in an increment of $\gamma$ in the sensory hue. This corresponds with Rood's results in so far as the unchanged quality of the greenish-yellow is concerned.

Grassmann's Laws of Color Mixture...... We may consider here two of Grassman's four laws of color-mixture. The first law of Grassman is of no particular importance and is obviously fallacious. It states that "every impression of light may be imitated by mixing a homogeneous color of a certain intensity with colorless light of a certain intensity." The sensory hue purple, of course, cannot be induced by any homogeneous light. The second law asserts that "if in a mixture one component be continuously varied the appearance of the mixture will likewise vary; unequal lights mixed with equal lights produce unequal mixtures." Since in our hypothesis the sensory hue depends entirely upon the relative states of excitation of the five molecular resonators, and since no change in the wave-length of the stimulating light can occur without change in these relations, our postulates are quite in harmony with Grassmann's second law. The third law says: "Lights which appear equal give, when mixed, equal mixtures. A corollary is that proportional increase of each com-
ponent does not destroy a match." It is clear that for low intensities this law is also consonant with our theoretical results, but that for high intensities we should not expect it to hold. As a matter of experiment the law does not receive complete verification. Thus Tonn finds that the complementary of a light of $\lambda = 670.8$ changes from $\lambda = 511.8$ to $\lambda = 547.3$ when the intensity of the lights is reduced to a fortieth. The hypothetical cause of this change is self-evident. The complementary of $L_{670.8}$ at high intensities must introduce a rather powerful $m_b$ excitation to complement the strong $m_y$ which we have given reason to suppose always occurs in conjunction with $m_r$ at normal intensities. At low intensities, however, $m_y$ falls below the threshold, so that for complementation the $m_b$ factor is no longer required, and the position of the complementary light shifts to the left in the spectrum. Tonn states that the complementary of $L_{586.5}$ shows no change in position with changing light intensity. This fact, also, is in harmony with our hypothesis, since this is (approximately) the point of intersection of the $m_r$ and $m_b$ curves shown in Fig. 9. Neither the $m_r$ nor the $m_g$ excitations are involved in this region, so that the complementary excitation is a relatively pure $m_b$.

Sensitivity to Changes in Wave-Length. The facts of difference-sensitivity with respect to wave-length have been much studied. The accompanying curve (Fig. 12) shows the distribution of this function in the spectrum. The observation that the highest difference sensibility occurs in those parts of the spectrum possessing the highest luminosity and least chro-

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Fig. 12.

THE MAGNITUDE OF JUST PERCEPTIBLE DIFFERENCES IN WAVE-LENGTH AS A FUNCTION OF THE WAVE-LENGTHS.

Abscissae: Wave-lengths of Light in $10^{-7}$ cms.

Ordinates: Just Perceptible Wave-length Differences, i.e., Changes in Wave-length Just Sufficient to Induce Discrimination Between Sensations in Point of Sensory Hue.

Curve A is that of a normal observer ("normal trichromatic.")

Curve B is that of a photerythrous observer ("dichromatic, green blind.")

ma may or may not be taken to mean that the discrimination li-
men which is active (cf. page 283) is $\Delta c_w$ rather than any $\Delta c_h$,
but in either case our postulates are able to account for the
facts. It will be seen that for the normal observer (curve A,
Fig. 12) the regions of greatest sensibility for differences in
wave-length are about $\lambda = 580$ and $\lambda = 490$. A glance at our
resonance function diagram (Fig. 9, page 330) will show that it
is just in these regions that the greatest shifting in the compon-
ention of the visual impulse should occur. In the first region
both the $\dot{m}_y$ and the $\dot{m}_g$ excitations are rising while the $\dot{m}_p$
excitation is falling; in the second region the $\dot{m}_g$ and $\dot{m}_y$ excita-
tions are falling while the $\dot{m}_b$ excitation is increasing. It should be
borne in mind that in so far as they affect the visual cerebro-
sis the resonance functions involved are not those represented
in Fig. 9, but are of the top-flattened sort pictured in Fig. 10.
The points of maxima and intersection remain approximately the
same, but the relative values of the resonance gradients at differ-
ent points are only related in a general directional sense with
those indicated in Fig. 9. The obvious effect of this top-
flattening of the function will be to locate the position of maxi-
um resonance gradient (the point of flexure of the curve of the
complete stimulation function, cf. page 326) much nearer the base
of the curve than appears in Fig. 9. This will have the effect
of concentrating the hue changes still more in the regions about
$\lambda = 580$ and $\lambda = 490$. It is clear that when—as between $\lambda = 750$
and $\lambda = 660$, one or more curves are rising without any correlat-
ed fall of another curve, the hue changes will amount to altera-
tions of chroma, only, the constitution of the sensory hue remain-
ing constant, -- or nearly so. The results of Brodhun, which we have figured (page 352) for one observer (and for a green-blind observer) show that the discrimination limen involved was of the Δc₁ order. We have already pointed out, however, that in the regions about \( \lambda = 580 \) and \( \lambda = 500 \), our postulates call for a relatively low chroma and, on certain conditions, high luminosity. Since the absence of hue (H) in these portions of the spectrum is an indication of a relative predominance of the achromatic visual system in the response, and since our evolutionary study of this system will lead us to believe that its functioning is based wholly upon sensibility for quantitative differences (cf. page 362), it seems reasonable to suppose that the tendency towards high difference sensibility in the spectral regions now under discussion is augmented by the changes in chroma and luminosity which occur in these portions of the visible spectrum.

On Primary Colors.... This point seems an appropriate one at which to introduce a few remarks on the conception of primary colors. From our point of view a sensation possessing would be a primary color, but a single one of the hues, and quite free from either \( \tilde{R} \) or \( W \), if by the indefinite word color we denote any concrete visual sensation possessing any degree of chroma. A primary light might be defined as the light possessing a wave-length corresponding with the maxima of the resonance functions of the chromatic resonators; thus--as our hypothesis is at present constructed--\( L_{657} \), \( L_{562} \), \( L_{538} \), and \( L_{454} \) might be defined as primary lights. These conceptions, however, would be of very little use in our discussion; on the other hand, the persuasion, which might be engendered, that these lights were in some way elementary or related in a peculiar
way with the visual process would be apt to prove positively misleading. On account of the Fechner's law top-flattening of the resonance function curves, these maximum points have very little significance. Hering's insistence upon the definition of primary spectral lights has led him into unnecessary difficulties with the critics. Hering's theory starts with the assumption that the four psychological hues—as we have defined them—are primaries; it terminates with the assertion that the primary lights are:

(1) for R: a light containing a certain amount of "blue" but mainly made up of waves from the extreme low frequency end of the spectrum, (2) for Y: \( L_{574.5} \), (3) for G: \( L_{495} \), and (4) for B: \( L_{471} \). Now the spectral light \( L_{495} \) induces a blue-green, not a pure G. No real inconsistency is involved, however, as soon as the meaning of these primary lights is understood. Our own hypothesis is essentially the same as Hering's so far as the actual processes of color or hue antagonism in experiment are concerned. Hering desires that his primary lights should be complementaries, and it turns out that the lights inducing relatively pure hues are not complementary. The reason for this can readily be gathered from an inspection of our diagram (Fig. 9, page 330). Although the ions \( I_{r^+} \) and \( I_{g^+} \) are strictly complementary, the lights \( L_{657} \) and \( L_{538} \) are not so, for the former excites a strong production of \( I_{y^+} \) ions which must be counterbalanced by a correspondingly powerful addition of \( I_{b^+} \) ions; to accomplish this we must move the complementary light over into the blue. The causes which lead Hering to select the lights above specified as primaries are undoubtedly mixed; the facts of color campimetry are probably dominant. These will be discussed in relation to our own hypothesis.
in another place (page 467). It is to be noted that the primaries of the modern Young-Helmholtz hypothesis possess peculiar properties; for example, the primary "red" of this hypothesis, like Hering's, requires an admixture of "blue" light. The circumstances which lead to this definition speak strongly for our view that the spectral red is throughout its extent based upon an \( \bar{m}_y \) as well as an \( \bar{m}_r \) excitation. To get a pure \( R (\times B \times W) \) the \( \bar{m}_b \) process must be sufficiently augmented to take out the \( I_{y^+} \) by the complementation reaction.
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5. LEHMANN, ALF.: Ueber die Anwendung der Methode der mittleren Abstufungen auf den Lichthein; (1898); Philos. Stud., Bd. 3, S. 497-533.


Section XXXIII: The Problem of Sensory Luminosity.

The Mechanism of Luminosity.....

The problem which it is now our purpose to briefly consider is one which has received a great deal of attention in the hands of Hering's school of visual physiology, but which has been sadly neglected by the Young-Helmholtzians. The reason for this is apparent. The Young-Helmholtz theory has no explanation to offer either for the sensation quality of whiteness nor for any of its modes of production, while Hering's hypothesis is the direct outcome of an attempt to give an intelligible account of the underlying mechanism of this sensation attribute, of the process of complementation, and of the meaning of color luminosity. In our analysis of the elementary visual sensation we have defined the luminosity of the sensation as the product, \( tw \), where \( t \) represents the sensation tint, or degree of achromaticity—as it were—of the sensation, and \( w \) stands for the degree of whiteness within this achromaticity. Now according to our hypothesis (cf page 260) every element of the visual synergy possesses five components: \( Z_{cr} \), \( Z_{cy} \), \( Z_{cg} \), \( Z_{ob} \) and \( Z_{cl} \), the last being the cortical luminosity element. Now in our discussion of the evolution of the visual mechanism (cf. page 437) we shall find reason for supposing that there is a constant struggle going on between \( Z_{cl} \) and the other cortical elements for control of the motor mechanism of the nervous system, so that the luminosity element and the chromatic elements may be regarded as balanced against each other in the visual synergy. Now in sensation the functional predominance of the chromatic elements means high chroma, \( h \), while that of the luminosity element means high \( tw \); we have already pointed out, the
derived attributes, $t$ and $h$ are correlated with each other psychologically so that: $h_{\text{max}} - h = t$. We have supposed that the fundamental sensory attribute $b$ is paralleled psycho-physically by a relative negativity of the cortical element, so that $b = i_- = k - i_+$ where $i_+$ and $i_-$ represent the concentrations of positive and negative ions—of any sort—in the cortical element, respectively. We do not imagine that there is ever any actual negative charge upon the cortical cells, i.e., any unbalanced negative ions; absolute blackness, $b_{\text{max}}$ would be paralleled by a neutral state of the cortical cells, an absence of all excitation, the absence of the synergy, and hence would be equivalent, over the whole visual field, to complete blindness; there would be no visual field. This does not mean that black is not a positive sensory quality, any more than it means that electrical equilibrium is the same thing as physical non-existence. It simply signifies that, as we have imagined it (cf. page 256), the visual synergy, and hence the visual consciousness, is dependent upon the existence of an electrical field. Now it is obvious that the "excitation for black", being the absence of excitation may be located in any or all of the components of the cortical visual element. The excitation for white, however, can only be located in the luminosity element, just as the excitation for red can only be referred to the $R$-element. The excitation of the latter element depends upon the presence in the cortical receiver (cf. page 261) of specific positive ions, viz., $I_{r+}$; the excitation of the luminosity element, on the other hand only demands the presence in this latter neuron (?) of some positive ion. For a description of the mechanism involved we must refer the reader once
more to page 260. If the concentration (initial cerebral intensity) of positive ions--of any sort--in the cortical receiver at any time be designated by \( c'_w \), we have: 
\[ c_w = k_{sw} c'_w \]
where \( c_w \) is the intensity of the excitation in the luminosity element, and \( k_{sw} \) is a constant. The cerebrosis intensities of the other components of the element of visual synergy will, similarly, be:
\[ c_r = k_{sr} c'_r, \text{ etc., where } c'_r, \text{ etc., are the initial cerebral intensities of the corresponding ions}, \]
\[ I_{r+}, \text{ etc. Obviously: } c'_w = c'_r + c'_y + c'_g + c'_b + c'_w'. \] It is impossible, however, that complementary ions should be simultaneously present on account of the complementation reaction which goes on in the large ganglion cells of the retina (and possibly in other regions of the impulse), so that if \( c'_r \) has a finite value \( c'_w \) will be zero, and similarly for \( c'_y \) and \( c'_b \) (cf. page 272). It appears from the construction of the cerebral apparatus, then, that chroma and luminosity should be proportional rather than reciprocal in their relations. The reciprocal relationship is entirely an outcome of the retinal mechanism of complementation, and it only holds psychologically within certain limits and under certain conditions. Given the presence of chromatic ions alone in the cortical receiver, the luminosity of the induced sensation will be strictly proportional to its chroma. It will be perceived, however, that with the visual mechanism as a whole as we have postulated it, a pure chromatic content of the cortical receiver is out of the question. As we increase the stimulation, moreover, the Fechner's law complementation effect will introduce an increasing number of \( I_{w+} \) ions so that as the relative number of chromatic ions decreases--owing to their removal in the complementation reaction--the relative numb-
er of achromatic ions will increase. From this it does not follow, however, that the excitation $c_w$ will increase absolutely—and hence that there will be an augmented sensory luminosity—since $c_w$ depends upon the absolute concentration of positive ions in the cortical receiver, and this quantity is not determined by the intensity of the visual impulse at the cortex, alone, but depends also upon the cortical dissipation of these ions from this element. If $I_{w'}$ happens to possess a higher dissipation coefficient (cf. page 251) than the chromatic ions, there may even be a decrease in the absolute value of $w$ for the sensation.

The "Specific Brightness of Colors" ............... It will be seen that our hypothesis involves a conception of specific luminosity, or—to use Hering's term, "spezifische Helligkeit,"—for every simple hue. This means that, with the visual mechanism constructed as we have figured it, it is impossible to experience a sensation which does not exhibit the attribute $W$ in a certain degree. This fact—or hypothesis—does not, of course, have any effect upon our capacity to discriminate between the hue and the whiteness, since we are able to make them vary independently of each other. We may define the specific luminosity, $j$, of any hue as the "whiteness ratio" of the sensation quality in which the hue appears, when the cortical receiver is free from ions other than those corresponding with the hue in question.

Thus the specific luminosity of a certain hue, $H'$, may be defined as $j_{h'} = w_{h'}/h'$, where $w_{h'}$ is the whiteness of the sensation under the conditions specified, and $h'$ is the "degree" of the particular hue $H'$. Thus we have: $j_{h'} = \frac{w_{h'}}{h'} = \frac{c_w}{c_{h'}} = \frac{k_{sw}c'_{h'}}{k_{sh}c'_{h'}} = \frac{k_{sw}}{k_{sh}}$. 
Luminosity and Intensity of Stimulus  

It is seen that, other things being equal, as a sensation gains in chroma it also gains in luminosity. But it can only gain in chroma by reason of an increase in the intensity of the light stimulus applied to the retina, and as we have seen this intensity augmentation of the stimulus means a lowering of the proportion of chromatic ions in the impulse. Tint and luminosity are not identical; a perfect black would have absolute tint, but zero luminosity. Hence the law of correlation between tint and chroma holds in spite of the cortical proportionality between \( c_w \) and \( c_n \).

Tint loses first by reason of the decreasing blackness, and secondly, with the increasing whiteness it gains by the decline of the sensation chroma through the influence of the complementation reaction. At very high intensities the sensation is once more purely achromatic, no matter what the nature of the light stimulus.

The Relative Luminosities of the Spectral Colors...  

A great deal of attention has been paid by experimenters to the problem of the relative luminosities of different parts of the visible spectrum. We must consider this question somewhat summarily. A glance at Fig. 9 will cause it to appear likely that—if the resonance functions there represented are correct—the region of maximum brightness will be near the long-wave-length end of the spectrum. As a matter of fact, however, this appearance will be entirely deceiving, so far as the implications of our fundamental postulates are concerned. It is true that in order to determine the luminosity of any particular spectral region one has theoretically only to find the sum of the excitations
postulated for that region, but the curves in Fig. 9 tell us nothing concerning the quantitative constitution of the impulse at intensities of stimulation greater than unity. These curves are intended to represent the constants and the general form of the several resonance functions. The maximum ordinate of each function is intended to show the relative light sensitivity of the resonator whose properties are described by it. This light sensitivity is only one of the factors which determine the intensity of the visual impulse at the retina (for the ions of the special resonator considered) at high intensities. This we have seen in our study of the causes underlying Fechner's law. (cf. page 317). The Fechner's law maximum for the $m_r$ excitation may happen to be much below that for the $m_y$ excitation in spite of the fact the light sensitivity of the $m_r$ substance is much greater than that of $m_y$; in other words, the rate of decrease of the effective light sensitivity with increasing light intensity may be so large in the case of $m_r$ that the $m_y$ excitation soon catches up with the $m_r$. Now our evolutionary argument (page 378) will make it clear that the Fechner's law maxima for $m_r$ and $m_g$ must be normally identical, those for the other two complementary dissociations being also equivalent. An equality of this sort is essential in order that exact complementation should result from the use of stimuli of high intensities, daylight, etc. (cf. page 337). No special assumptions need to be made to explain the existence of an equality of this sort, since its production is a simple matter of evolutionary adaptation involving nothing more than a variation and selection of the values of the several constants ($k_r, m$, etc.) involved in each case. It does not follow
of course that because the maximal excitations of the complemen-
tary retinal resonators are equivalent within the complementary 
pairs, they are also equivalent altogether. However, the explana-
tion which we shall give of the fact that in the prismatic (visi-
ble) spectrum the region of maximal luminosity is in the yellow 
depends upon the supposition that when the light intensities em-
ployed in retinal stimulation are relatively high—as in the com-
mon solar spectrum—the total intensity of the resulting visual 
impulse is a function of the light intensity only. This cannot 
apply, of course, to the extreme regions of the spectrum, since 
here all of the resonators cease to be affected. The maximum of 
luminosity in the yellow is thus to be explained by showing that 
in the ordinary prismatic spectrum the intensity of the rays 
falls off very rapidly, owing to increased dispersion, as the 
short wave-length end is approached. The accompanying graph (Fig. 
13, page 365) shows that the dispersion begins to rise in the 
orange (\( \lambda = 650 \) to \( \lambda = 600 \)), and hence that—provided we assume 
uniform intensity of the analyzed light with respect to change 
in wave-length—in this region the intensity of the stimulus be-
gins to decrease. This decrease becomes very marked as the so-
dium line (the point of maximum luminosity) is passed. In our 
opinion, the maximum in the yellow is to be referred to the com-
bination of this waning of the stimulus with the coincident wax-
ing of the \( m_x \) and \( m_y \) resonances. This opinion is confirmed by 
the fact that—so far as the observations of the present writer 
are able to show—the middle stretches of the diffraction spec-
trum, in which the dispersion (effective) is the same for all 
wave-lengths, are uniformly luminous. The experimental results
Fig. 13.

GRAPH SHOWING RELATIVE DISPERSION OF LIGHTS OF DIFFERENT WAVE-LENGTHS IN THE PRISMATIC SPECTRUM.

Abscissae: Wave-lengths of light in $10^{-7}$ cm.

Ordinates: Space interval for a difference of 10 wave-lengths. Inches.

The above graph represents a wave-length scale interpolated in the spectrum chart published by the Prang Educational Company, Boston, Mass.
of Draper, also indicate that in the diffraction spectrum the colors are uniformly luminous. It should be noted, however, that in the event of a failure of the explanation here given of the location of the point of maximum luminosity in the normal type of visual response, our hypothesis offers the possibility of a physiological explanation of the effect, for a glance at Fig. 9 will show that in the region in question (near $\lambda = 590$) three excitations are strongly represented, while in other regions not more than two are simultaneously present at a high intensity.

It is to be kept in mind that the problem of the relative chroma values of the spectral colors is not necessarily bound up with that of their relative luminosities. We have already pointed out (page 337) that the spectral Y and BG are of the lowest chroma, and have accounted for this fact by the circumstance that maxima of complementation occur at about $\lambda = 580$ and $\lambda = 500$, as shown in Fig. 14.

The well known Purkinje phenomenon need not claim the attention of our thought for long. The decline in the excitation of the chromatic resonators which occurs with decreasing light intensity is accompanied by a rise in the excitation of the $M_w$ element. This, as shown in Fig. 9, has a maximum at $\lambda = 520$, and since $M_w$ is very little acted upon by the long wave-lengths the point of maximum luminosity must necessarily shift towards the blue. The spectrum of lowest intensity—the so-called achromatic spectrum—depends for its induction upon the excitation of the resonator $M_w$, only, and with but a single excitation present the decreasing intensity towards the short wave-length end of the physical spectrum can have very little effect upon the absolute position of the maximum. The
Fig. 14.

CURVE SHOWING INTENSITY OF THE COMPLEMENTATION REACTION WITH STIMULATION BY THE USE OF LIGHTS OF DIFFERENT WAVE-LENGTHS..........

Abscissae: Wave-lengths of Light in $10^{-7}$ cms.

Ordinates: Number of equivalents of $I_w^+$ produced per second per unit light intensity under conditions specified in Fig. 9.

The above curve was constructed by taking off the ordinates of the curves in Fig. 9 by the use of dividers, and in accordance with our definition of the complementation reaction.

The chromas of the spectral colors are reciprocally related with the ordinates of the above graph.
excitation $m_w$, of course, yields $I_w$ ions alone, so that in the achromatic spectrum the chroma is zero at every point, and the only maximum possibly observable is a maximum of luminosity. As stated in another place, the writer considers $m_w$ to be identical with the visual purple of the rods, and is inclined to accept upon their face value all of the experimental and theoretical results of von Kries and others which go to show that the Purkinje phenomenon and related effects only occur in portions of the visual field corresponding with rod-inhabited regions of the retina.

The Principle of Flicker Photometry............ On page 307 we have discussed the principles which we suppose to govern the appearance and disappearance of flicker under intermittent stimulation. Now it is a well known fact—the basis of the method of measuring the luminosity of colors designated as "flicker photometry"—that the rate of stimulation which coincides with the vanishing of flicker in the sensation is determined by the luminosity of the sensation, only. This fact may be explained in terms of our hypothesis by noticing that, on account of the genetic history of the achromatic cortical mechanism, our capacity for discriminating between differences of luminosity, physically, between differences of $c_w$—must be greater than that which has reference to hue or chroma. According to König, 660 different degrees of luminosity are discriminable, while only 160 distinct sensory hues can be made out. Kulpe puts the number of "Helligkeitsstufe" at 810, and of sensory hues at 150. Without deeper analysis, this may be taken to mean that the luminosity limen, $A c_w$, (cf. page 263) is much smaller than the cor-

1 KÖNIG, A.: Über die Anzahl der unterscheidbaren Spektralfarben und Helligkeitsstufen; (1895); Zeits. f. Psych. u. Physiol. d. Sinnesorg., Bd. 8, S. 375-381. (over)
2. KULPE, O.: Outlines of Psychology, trans.; (1895); N. Y.

...
responding quantity for any of the simple chromatic cerebrose. But we have seen on page 307 that in the last analysis flicker must be adjudged a function of the discrimination mechanism, and that the velocity of the rotating disk at which flicker just disappears must be determined by the value of the cortical discrimination limen which is involved. The complexity of the cortical mechanism makes it necessary that several such limina should be concerned, but in this case, the disappearance of flicker will be governed by the activities of the most sensitive of the discrimination structures, and this--we have seen--is the achromatic discrimination element. But if this is the case (cf. page 307) the rate of intermittent stimulation at which flicker vanishes must be a function of the intensity of the achromatic cerebrosis, alone, so that this critical rate becomes a means of measuring luminosity.

Grassmann's Fourth Law of "Color Mixture".... Grassmann's fourth law of "color mixture" states that "the total intensity of a mixture is the sum of the intensities of the lights mixed." Put in terms of our own theory this means that the luminosity of a visual sensation is a function of the intensity, e, of the light stimulus, only. In order that this should be in harmony with our postulates we have merely to suppose that the rates of dissipation of the various visual ions from the cortical receiver are approximately the same. In this case, since in case of (say) a complementary light mixture, the number of ions reaching the cortical receiver will be the simple sum of the number which would have arrived had either of the two lights been employed separately, the total positive charge upon the element will
be the sum of the charges which would have existed with the employment of the two stimuli apart from each other. It is true that for high intensities this cannot be exactly the case, but it is not certain that the fourth law holds for all intensities, and if it does so hold a simple mathematically representable alteration in our assumptions will place them in complete harmony with this particular set of facts. It will be remembered that the intensity of the achromatic cerebrosis is determined by the positivity of the cortical receiver, rather than by the qualitative nature of the ions which are present. Notice should be taken of the fact that assumptions with reference to the dissipation coefficients of the various visual ions in the cortical receiver do not--superficially, at least--imply anything concerning the coefficients of dissipation of the same ions (or others) from the chromatic or luminosity elements.
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Section XXXIV : The Explanation of Simultaneous Contrast.

"The Proper Light of the Retina"...

When the retina is entirely unacted upon by light one might expect that the cerebrosis intensities of all five components of the visual cerebral excitation would be zero. Examination of our postulates will show, however, that this cannot be the case, for we have supposed—with all reason—that each of the visual ions possesses a certain normal, unstimulated, ionization (cf. page 217). This being the condition of affairs in the retinal elements, visual nerve currents must continually be travelling centralward, so that the visual cerebrosis can never be entirely negative, while the retinal mechanism is intact. The existence of this constant normal visual excitation has been mathematically indicated in the form of the equation: \( \dot{m}_a = (k_1 + \text{eq } f_\lambda (\lambda))m - k_2 \dot{i}_{1+}, \) \( k_1 m - k_2 \dot{i}_{1+} \) being the unstimulated rate of dissociation at any time. In our Fig. 9 this constant has not been adequately represented.

If absolutely no visual impulse existed the sensation quality over the entire visual field should be utter black, if no other source of cortical excitation is active. As a matter of fact when the retina is wholly unstimulated by light the quality of the sensation filling the field is gray, i.e., it possesses a relatively high luminosity. This so-called "proper light of the retina" is, of course, to be attributed to this normal ionization of the molecular resonators. Certain implications of the usually achromatic character of this native sensation will be shortly considered.
"The Central Gray"........ It is probable that the spontaneous activity of the retina is not the only source of a non-functional excitation of the visual cortex. The ionic nature of the luminosity element which we have postulated (cf. page 260) is such as to invite slight disturbances in electrical potential resulting from minor physiological changes taking place in the cerebral tissues. Moreover, the visual mechanism in the cerebrum is only a part of a vast and very active synergy, the other elements of which must inevitably have some effect upon the visual cerebrosis itself. The various synaesthesias and subjective color phenomena in general demonstrate the actual existence of this functional—or even accidental—interdependency between different factors in the central process. We are right, then, in believing that, even with complete extirpation of the retinas, some cortical excitation might be present. There would undoubtedly be a tendency, however, towards complete quiescence, so that the neglect of meaningless and slight changes occurring in the visual region would lead finally in total blindness to the disappearance of the visual field from consciousness.

The Induction of Black........ Since the normal unstimulated sensation quality is gray, exhibits the attribute W in a marked degree, it at first seems difficult to understand how it can be possible for any sensation to exist—in parallelism with the normal visual mechanism—which shall exhibit a lesser luminosity. It is perfectly obvious that in order that such a sensation should be induced the cerebrosis intensity parallel with the "proper light of the retina" must be lowered. How is it possible for this to take place under the influence of active retinal stimulation, the condition under which the sensory attri-
bute, E, most strongly appears? The answer is that it is a mat-
ter of contrast, a process in which the increase in excitation
of one region of the retina brings about a decrease in the excita-
tion—of the same sort—in the adjacent regions. Let us brief-
ly consider the nature of this process.

Simple Achromatic
Contrast. . . . . . . . .

In the first place, the simplest case
of simultaneous contrast may be analyzed.

This is the case of pure achromatic retinal "induction", in the
terminology of Hering, who has studied the effect in question in
great detail. We will take notice of the retinal rods only, and
consider that the only molecular resonator present is $M_w$. Let
$S_d$ denote the visual sensation situated at a specific point in
the visual field, and let $C_d$, $I_d$, $X_d$ and $L_d$ be the other factors
of the elementary visual response $V_d$ (cf. page 252). The sen-
sation existing in any closely adjacent region of the field may be
designated as $S_o$, and the corresponding factors of the response
$V_o$, by $C_o$, $I_o$, $X_o$ and $L_o$. Since $S_d = f(X_d)$ and $S_o = f(X_o)$, and
since these relationships are true quantitatively as well as
qualitatively slight attention may be paid to the intermediary
processes. Now imagine that an increase occurs in the intensity
$e_d$ of the light $L_d$; as a result the corresponding stimulation
process $X_d$ must increase in intensity. If we suppose that in the
beginning $X_o = X_d$, after the rise in the value of $e_d$, we must
have: $n_{ad} > m_{ao}$, hence: $t_{rd} > t_{ro}$. This means that the rate at
which $I_w^+$ ions are leaving the rod $Z_{rd}$ is greater than that at
which they are leaving the rod $Z_{ro}$. Since in the reaction:

$M_w \rightarrow I_w^+ + I_w^-$, $I_w^-$ ions are produced in number equal to
that of $I_w^+$, when equilibrium is established, the rate of dis-
sipation, $\rho$, of the negative ions through the retinal bacillary layer from the point $Z_{rd}$ must be greater than that taking place in the opposite direction. If this is the case, when equilibrium obtains--and before--the concentration of $I_{w'}^-$ ions in the rod $Z_{ro}$ must have increased over the concentration of the same ions which existed previously to the stimulation of $Z_{rd}$. But the state of ionization of the molecular resonator, $M_w$, in the rod $Z_{ro}$ depends upon the concentration of each of the ions, $I_{w'}^+$ and $I_{w'}^-$ in such a way that--conditions of stimulation remaining unaltered--at equilibrium we have: \[(k_1 + k_2)m_w = k_2I_{w'}^+I_{w'}^-\]. It is obvious then, that, an increase in $I_{w'}^-$ must be accompanied by a decrease in $I_{w'}^+$. Since \[I_{w'} = k_{Iw'}I_{w'}^+I_{w'}^-\] at all points in the retina, this lowering of $I_{w'}^+$ in $Z_{ro}$ accompanying stimulation of $Z_{rd}$ without concomitant equal stimulation of $Z_{ro}$ must result in a lessening of the $I_{w'}^+$ component of the visual impulse intensity, a corresponding decrease in the cerebroside intensity $c_{w'o}'$, and in $c_{wo}$. Parallel with this latter change there will be a decreased luminosity of the visual sensation $S_o$, which will be accompanied, of course, by the (stimulated) rise in the luminosity of $S_d$. This is the mechanism of simple achromatic simultaneous contrast. It is seen that this phenomenon depends upon the fact that stimulation of the retina always involves the production of an equal number of positive and negative achromatic ions, that while the positive ions are convected away along the nerve the negative ions are obliged to escape through the outer layers of the eye, and in doing this, in accordance with the law of chemical mass action, force back the ionization of the achromatic resonators in regions of the retina lying outside
that region which is being subjected to special stimulation.

The Equivalency of Complementary Chromatic Normal Ionizations....

We may now turn to the consideration of "color contrast." Since the unstimulated visual sensation is characteristically gray in its quality, it follows that the normal ionizations of the four chromatic molecular resonators, $M_r$, $M_y$, $M_g$, and $M_b$ must be so adjusted that the resulting components of the visual impulse at the retina, possess the relationships: $\theta_r = \theta_g$ and $\theta_y = \theta_b$. This adjustment does not depend upon actual equality of the ionizations themselves, but upon the relative values of the constants, $k_{rr}$, etc., which are involved, and it may be regarded as the outcome of an evolutionary adaptation, directed towards the elimination of color illusions; the hues must be made to depend upon the quality of the stimulus alone. Of course, if the above indicated equality obtains between the complementary components of the visual impulse at the retina, no chromatic ions can reach the cortex, and the induced sensation—of the normal, unstimulated, ionization of the chromatic resonators—will be gray, complementation ions, only, arriving at the cortex.

Complex Achromatic Contrast...........

It is clear that, as a result of the above arrangement, contrast due to the reciprocal reactions of adjacent retinal rods will not be the only possible type of achromatic contrast. Indeed, since it seems that the rods are practically non-functional in daylight stimulation, it must be true that the achromatic contrast most common in experimental studies is that which depends upon the activities of the chromatic resonators of the cones. A descrip-
tion of this complex type of B-W contrast need not be given, since it is identical in its mechanism with that of the simpler sort fully set forth above. Stimulation of the retinal cone $Z_{\mathbf{R}}'$ with a mixture of lights so balanced as to induce a complementation gray or white entails the movement of four sorts of negative ions radially from the stimulated point. The result will be that all four chromatic ionizations in the outlying cone $Z_{\mathbf{R}}'$ will be forced back in equivalent proportions, so that the change in the cerebrosis $C_{0}$ will be a decrease in the concentration of complementation ($I_{w}^{++}$) and luminosity ($I_{w}$) ions, only.

Chromatic Contrast. The physical mechanism of chromatic contrast is now self-evident. Suppose that $Z_{\mathbf{R}}'$ is stimulated with a homogeneous—or relatively homogeneous—light, $L_{\text{hm}}$. In this case there will be a spread of specific negative chromatic ions from the stimulated point, the disturbance of the normal ionization of specific chromatic resonators, a failure of the—unstimulated—complementation equilibrium, and the consequent induction of an sensory hue in the region of the visual field which is occupied by $S_{0}$ that is complementary with respect to the—stimulated—sensory hue of $S_{d}$. Imagine, for example, that the light, $L_{d}$, is $L_{700}$, and that the intensity of the light $L_{0}$ is $e_{0} = 0$. In the cone $Z_{\mathbf{R}}'$ there will be a marked augmentation in the rate at which $I_{r-}$ ions are being produced (cf. Fig. 9), a slighter increase in the rate of production of $I_{y-}$, and a negligible increase in the rates for $I_{g-}$ and $I_{b-}$. The result must be that in the cone $Z_{\mathbf{R}}'$ the reactions: $M_{r} \rightarrow I_{r-} + I_{r+}$ and $M_{y} \rightarrow I_{y-} + I_{y+}$ will be disturbed, while the other two reactions will remain practically as before. The concentration $i_{r+}$
in the cone $Z'_{g'}$ will be greatly diminished, while that of $I_{g'}$ will be practically unaffected. Consequently the complementation reaction between $I_{r'}$ and $I_{g'}$ in the corresponding element of the impulse will not be complete, a balance of $I_{g'}$ ions remaining, which pass to the cortex and are there paralleled by the presence of the hue $G$ in the quality of the sensation $S_0$. A similar argument makes it necessary to admit that in the same sensation quality there will be a certain amount of $B$--a certain intensity of blueness--corresponding with the decrease of the concentration $I_{y'}$ in $Z'_{g'}$. Clearly, then, simultaneous chromatic contrast will be a contrast between complementaries in every case.

Further Complexities Involved in Chromatic Contrast....

We have spoken of the mode of movement of the negative visual ions in the bacillary layer of the retina as if it were a simple matter of molecular diffusion. Of course this is not the actual state of affairs; if it were, we could hardly make any use at all of the explanation of contrast offered above, for the translation of molecules or ions by simple diffusion is excessively slow. It is obvious that the removal of positive ions from $Z_{rd}$ by the neuro-fibrillar mechanisms must leave $Z_{rd}$ with a negative charge, so that negative ions in this retinal element will be acted upon by an electric force tending towards dispersal. This force will be proportional to the concentration of negative ions present in $Z_{rd}$ above that present in $Z_{ro}$, and will be radial from $Z_{rd}$ if the remainder of the retina is uniformly excited.

Now if a negative potential exists at $Z_{rd}$ with respect to $Z_{ro}$, a positive potential must exist at $Z_{ro}$ with respect to $Z_{rd}$ so that not only will negative ions tend to move from $Z_{rd}$ to $Z_{ro}$,
positive ions, also, will tend to travel in the opposite direction. It follows that with unequal retinal excitation, ions of all species will be subject to migration, and that the decreased concentration of $I_{r+}$ ions in $Z_{R0}$ due to the influx of $I_{r-}$ ions will be still further diminished by the departure of $I_{r+}$ ions towards $Z_{Rd}$. A similar centripetal movement of the ions $I_{y+}$, $I_{b+}$ and $I_{g+}$ will occur, while an opposite, centrifugal, displacement of $I_{r-}$, $I_{g-}$, $I_{y-}$, and $I_{b-}$ will be brought about. The result will be that an augmentation of the original stimulation will ensue, accompanied by a generally decreased sensitivity of the surrounding retinal regions. The corresponding sensations will gain and lose in luminosity, respectively.

A Possible Objection to the Above Explanation...

In spite of the fact that relatively powerful intermolecular electric forces may be involved in the above postulated ionic movements it may still be objected that the translatory displacement of ionic masses is an exceedingly slow process, and that the almost instantaneous character of simultaneous contrast precludes the acceptance of the proffered rationale. In reply to this it must be admitted that the objection is a powerful one, but not conclusive as stated. The velocity at which ions travel in a medium is determined by two factors, the force which impels them and the resistance which they encounter. The forces involved in the present postulated case may very well be large, since they depend upon molecular and not upon molar properties of the living substance. But admitting that they could not reasonably be considered as sufficiently great to account for the "speed" of simultaneous contrast, we may still suppose the resistances in-
volved to be relatively small. Since contrast is obviously a
great aid in distinctness of perception, any peculiarity of the
retinal tissues favoring it would be preserved in the struggle
for existence. A molecular specialization of the cells of the
bacillary layer may very well have taken place in the course of
evolution which is analogous with that which we suppose to have
occurred in the development of nervous tissue. The only hypothe-
sis which is necessary is that of an abnormally long free-path
in certain directions under certain conditions. A Lack of
space and time makes it impossible for us to indulge in a discus-
sion of the quantitative basis of the so-called laws of contrast

The Quantitative Aspect. A few words upon this subject may, of Simultaneous Contrast however, be said. It has be shown
by experiment that in the case of chromatic contrast the effect
is proportional to the logarithm of the chroma of the sensation
$S_d$, and also that it is related in the same way with the area of
the image in which $S_d$ is the characteristic sensory element. 1
Both of these laws are obviously in general accord with our ex-
planation of the underlying mechanism of the phenomenon. The
higher the chroma of $S_d$ the purer the migrating ionic mass with
respect to particular ions; the larger the stimulated area the
larger the mass in question. On the other hand since this dis-
ersion of ions takes place in three dimensions, the effect pro-
duced at $Z_{pd}$ cannot be linearly proportional to the intensity,
or purity, of the process at $Z_{rd}$; but must be proportional in
some function such as that which we have derived to explain Fech-
ners law. Again, the fact that contrast depends upon contiguity
and the absence of boundaries favors our viewpoint.

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Section XXXV : The Explanation of Adaptation.

Chapter 20 : The Functioning of the Achromatic Resonator.

The Achromatic Resonator Does Not Function in Daylight......................
We shall suppose that the activity of the resonator $M_w$ is confined to conditions of feeble illumination. This means that when the retina is acted upon by intensive light stimuli, the concentration of this resonator in the rods becomes practically zero, and that it is not renewed. If this is actually the case we must suppose the condition represented to be the outcome of an evolutionary adaptation, the purpose of which is to free daylight vision of bothersome sensitivity. $M_w$—the visual purple—is obviously possessed of an extremely high light sensitivity. Consequently with high light intensities—such as those given in relatively feeble daylight—its excitation would be very near the maximum allowed it by our deductions with regard to Fechner's law, and as a result, under these conditions it would be of no use in the discrimination of differences in stimulus strengths, and would simply flood the visual field with a uniform brightness through which the images induced by the less light-sensitive resonators would be only faintly apparent, as in a luminous haze. Although, as we have seen (page 323) the concentration of the molecular resonator decreases with increasing light intensity, the rate of dissociation of the resonator cannot become less than that at which the original aesthesogens are renewed, without the entrance of some new causal factor. The nature of this factor we shall suppose to be describable as follows. It is a well-known fact
that intense lights act deleteriously upon nearly all living tissues, inhibiting their normal functions. In all probability this is due to changes produced in the vital enzymes which control the activities of these tissues. When the intensity of stimulation passes a certain limit, then, the achromatic aesthesogenase is so affected that it is no longer able to catalyze the aesthesogenetic reaction, and as a result the concentration of the achromatic resonator sinks to zero and is not again finite until the decrease of illumination renders the enzyme functional once more. A similar effect—"sblouissement"—is noticed at very high intensities of stimulation under the condition of daylight adaptation, showing that the chromatic aesthesogenases are affected in a similar manner. The achromatic aesthesogenase, we must imagine, is especially sensitive to inhibition by light. As we have suggested, this is no doubt in part teleological.

Question of the Absolute Intensity of the Dark... Adaptation Cerebrosis...

It is apparent from the above explanation that we absolute intensity of the cerebrosis occurring under the influence of feeble illumination may be comparable with that which is produced by much stronger illumination. The Purkinje phenomenon, then, (cf. page 366) is not merely a shift of relative luminosities; it is also a change in absolute luminosity values. "Dazzling" is the visual consciousness which—in one instance, at least,—accompanies the very rapid destruction of $M_w$ which takes place when a light of daylight intensity is suddenly thrown upon the dark adapted retina.

Physical Properties of the Visual Purple.............

There are certain physical characteristics of the visual
purple which confirm our theory of the action of the light sensitive substances of the retina. Laying to one side as too completely demonstrated to deserve debate the facts that the light absorption curve and other optical properties of the substance in question correspond very accurately with the curve $W$, which we have drawn in Fig. 9, let us take note of the behavior of the pigment under the influence of light in general. It is found that a solution of the visual purple ($W$) which has been bleached by exposure to the rays of the sun, for example, if placed in the dark will again become purple. This has been ascribed to the presence in the solution of the achromatic aesthesogenase, rhodophylin, but from our point of view the bleaching must be considered simply as a process of thorough electrolytic dissociation of the pigment under the action of the light; when this action is suspended the chemical change naturally turns in the opposite direction, the condition of normal ionization being restored. If a section of the retina is bleached, however, regeneration of the pigment will not occur in the dark unless the retinal fragment is placed in contact with the pigmented epithelium. We may explain this by observing that when the bleaching—or dissociation—is brought about within the rod segments themselves, the positive ions are removed from the chemical system by the action of the optic fibres, so that when the light is shut off, no reversal of the reaction can transpire, because the requisite factors have been taken away; new aesthesogenetic material is necessary; this demands the cooperation of the epithelium.

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Chapter 21: The Explanation of the Phenomena of Chromatic Adaptation.

We have seen on page 323 that the retinal concentration of any molecular resonator is a function of the concentration of its underlying aesthesogens, so that:

\[ m = \frac{k + k \overline{AB} \overline{C}}{k + k_e} \]

\( e \) being the intensity of the stimulating light. Since the rate of dissociation of the resonator is relatively proportional to \( m \)--so that \( \dot{m_a} = (k_1 + eq f_r(\lambda))m - k_2 i_1 \)--and since the intensity of the corresponding component of the visual cerebrosis is similarly proportional to \( \dot{m_a} \), it follows that any change occurring in \( \overline{AB} \) and \( \overline{C} \) will be reflected by a change--in the same sense--of \( e \). \( \overline{AB} \) and \( \overline{C} \)--the aesthesogens--are constantly being furnished to the retinal elements by the lymph (cf. page 163), but we have no reason for believing that the rate at which they are supplied will be strictly proportional to the rate at which they are being consumed; there will undoubtedly be a physiologic tendency in this direction, but it will not be entirely accurate, and will possess definite limitations. Hence we must infer that when stimulation has for a long period been non-intensive, \( \overline{AB} \) and \( \overline{C} \) will have high values, but that after continued stimulation with light of relatively high intensities, their values will be lowered. This change in the concentrations of the aesthesogens as the outcome of variations in degree and duration of stimulus we regard as the principal basis of the phenomena usually grouped under the head of visual adaptation. Two other effects
which are of importance are the inhibition of the aesthesogen-
ases, mentioned in the preceding chapter, and the temporary de-
crease in $m$ which occurs under the influence of definite light
intensities in accordance with the mathematical relation given
above.

Achromatic Adapt-
tation......... 

When the retina is permitted to rest
during a considerable period the concentra-
tions of all of the four pairs of aesthesogens—neglecting the
achromatic aesthesogens—$: \overline{AB}_r, \overline{UV}_r; \overline{AB}_y, \overline{UV}_y; \overline{AB}_g, \overline{UV}_g; \text{ and } \overline{AB}_b, \overline{UV}_b;$
will increase. As a result there will be a gain in sensitivity
to light in general, and a consequent lowering of the absolute
threshold for the non-dark adapted eye. Similarly, prolonged
but moderate activity of the retina will bring about a general
lowering of these concentrations and a raising of the threshold.
All of these effects will be achromatic, and should not be ex-
pected to influence the sensibility to different homogeneous
lights in any very strongly selective fashion.

Selective or Chromatic Adaptation..............

Suppose, however, that the re-
tina is acted upon for a prolonged
period by a homogeneous light of marked intensity. In this case
there should be a differential change in the aesthesogenic con-
centrations with the result that upon stimulation of the same
retinal region with other lights abnormal effects will be ob-
tained. Carl Hess found that after fatiguing the retina with
light of approx. $\lambda = 700$, stimulation with $L_{400}$ induced a BG.
The original effect was a decrease in $\overline{AB}_r$ and $\overline{UV}_r$, by reason of
the high selective resonance of $M_r$. Examination of Fig. 9 will
show that the resulting depression of the $M_r$ curve would place

(over)
HESS, CARL: Ueber die Tonänderungen der Spectralfarbung durch Ermüdung der Netzhaut; (1890); Leipzig, 32 S.
it below the $M_g$ line, so that the only effective excitations
which could take place under the influence of $L_{400}$ would be $m_b$
and $m_g$. This adaptation phenomenon is, then, a corroboration
of our theory with reference to the meaning of the sensory hue
violet (page 339). Marie Bokowa found that after wearing ruby
red spectacles for a long period normally red objects appeared
yellow. This is easily explained by our figure (Fig. 9) the
relative excitations of $M_r$ and $M_y$ being altered in the long wave-
length end of the spectrum by the decrease occurring in $\bar{ab}_r$
and $\bar{c}_r$, or the relative increase in $\bar{ab}_y$ and $\bar{c}_y$. According to Hess
stimulation with $L_{400}$ (approx.) followed by the application of
$L_{700}$ induces an RY. This again is in harmony with our postu-
lates, the principal effect of $L_{400}$ being a decrease in $\bar{ab}_b$ and
$\bar{c}_b$. Fatigue with $L_{450}$ gives a similar response to $L_{700}$; to
$L_{400}$ both Exner and Hess report a sensation quality of R. This
is immediately demanded by our diagram. von Kries and Hess
find that spectral Y and B undergo little change with adaptation.
This is to be expected if the lights are so chosen that they
coincide with the points of intersection of the $M_r$ and $M_g$ curves
in each case. Fatigue with $L_{green}$ is said in certain cases to
cause stimulation with the same light to induce a BG, and in
other cases to bring about no change. The exact result obvious-
ly depends upon the particular $L_{green}$ selected. The experi-
ments of G. J. Burch are not so clearly in harmony with our pos-
tulates. This observer employed very powerful lights in the
fatiguing process.1 When waves falling between the Fraunhofer

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3 W.H.R.R., p. 1110.  4 BURCH, G. J.: Journ. of Physiol. (1898); vol. 22, p. xii f.
lines A and B were used, only G, B and violet could be perceived in the visible spectrum. Fatigue with lights from near the E line caused the green to vanish, and with it the yellow. This disappearance of Y in each case we must ascribe to the fact, represented in our diagram, that $M_y$ is strongly excited by both the long and the relatively short waves, from $\lambda = 700$ to $\lambda = 500$. As a result adaptation to the very intense stimuli employed by Burch would involve a very marked decrease in the aesthesogens of $M_y$ along with those of either $M_g$ or $M_r$. The failure of the violet to alter may be accounted for by noting that the observer reports the presence of a "strong subjective glare" of the color employed in the adaptation process. In the case of adaptation to the long wave-lengths the subjective R which existed would easily cause a retinal $m_g$ to be cerebrally mistaken for a violet inducing stimulation. Burch admits that it is difficult to give an exact description of the hues experienced, and in the case of fatigue to L green the violet of the visible spectrum is characterized as "dull and dirty." The results of Hess were obtained by an application of exact methods of color matching, only a portion of the retina being fatigued. It will be impossible here to discuss in greater detail the manifold changes which occur as the outcome of specific chromatic adaptations of the retina. It must suffice to have indicated the general consonance of our hypothesis with the facts; upon the chemical theory of visual response, adaptation is to be expected.
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Chapter 22: The Negative After-Image.

Basis of the After-Image

The negative after-image is obviously dependent upon the negative adaptation of a delimited portion of the retina. Within a certain retinal region which has been acted upon by a stimulus different in some regard from that which has been at work upon the adjoining regions, the concentrations of the aesthesogens--or other factors--have suffered a specialized change which causes the corresponding portion of the visual field to present qualities different from those appearing in other portions of that field, when, finally, the retina is subjected to uniform stimulation. We have seen that there are at least three possible bases of the phenomenon of adaptation which are afforded by our theory. The most important of these we have considered to be the lowering in the concentration of the specific aesthesogens under the influence of continued stimulation. This acts to reduce the concentration of the corresponding resonators, and thus to decrease the effective light sensitivity of the retinal element to particular types of stimulus. But we have also seen that the concentration, \( m \), is lowered by the mere presence of a light-stimulus. This is shown in the relation:

\[
m = \frac{k + k \overline{sb} \overline{c}}{k + k e}
\]

\( e \) being the intensity of the light which is acting. The third possible basis of adaptation is inhibition of the aesthesogenases.

The After-Image Following Brief Stimulation

Since the stimulation conditions giving rise to the after-image are identical with those which obtain along with simultane-
ous contrast, the same method of symbolism may be employed in the discussion of the after-image process which was employed in the consideration of simultaneous contrast (cf. page 376). We will suppose that the retinal element $Z_{x'y'd}$ is acted upon for a certain time by a specific stimulus, the adjoining element, $Z_{x'o}$ being unstimulated. The original physical image is then removed and the retina subjected to uniform conditions of stimulation, --in general, absence of all illumination. Now if $Z_{x'y'd}$ is stimulated with daylight for a brief interval, the concentrations of all of the molecular resonators will be decreased in accordance with the equation given on the preceding page; in $Z_{x'o'}$, on the other hand, there will be an increase in the resonator concentrations, due to the contrast ions which radiate from the stimulated element, and force back the normal ionization in the first element. When the light $L_d$ is removed, therefore, all of the retinal impulse intensity components of $I_d$ will be decreased, and all of those of $I_o$ will be increased. Consequently, in the visual field, $S_d$ will be less luminous than usual--in the proper light of the retina--while $S_o$ will be more luminous. This effect will be short lived, since the normal equilibrium will be almost immediately regained, when $e$ is removed. With brief stimulation it is impossible that the concentrations, $\overline{ab}$ and $\overline{c}$, should be noticeably affected. If the light $K_d$ is not daylight, but is relatively homogeneous in character, only one resonator will be strongly affected, and the depression of its normal concentration will disturb the normal complementation equilibrium in such a way that ions complementary to those derived from the resonator in question will be permitted to pass through the retinal ganglion cells, and the after-image which appears as $S_d$ in the visual
field will be complementary in sensory hue to the original $S_d$, accompanying stimulation.

After-Images Following Prolonged Stimulation. The explanation of the production of negative after-images which remain in the visual field for several minutes—or even hours—is identical with that given above for momentary after-images, except that in this case the effect is to be ascribed to the decreased concentrations of the aesthesogens. It is unnecessary to enter into a detailed description of the process since its mechanism is in all respects the same as that indicated above or which is active in the production of simultaneous contrast, either chromatic or achromatic. An achromatic $S_d$ will be succeeded by an achromatic after-image—a relative lack of luminosity—because the concentrations of all of the aesthesogens will be lowered; a chromatic $S_d$, on the other hand, will be followed by an after image complementary in hue to itself, because only its own characteristic aesthesogen will have materially suffered in concentration, and as a result, complementary ions will reach the cortical receiver.

Chromatic Fading of the White Light After-Image............. If, as our hypotheses make it necessary to suppose, an achromatic after-image depends upon the exhaustion of either two or four specific aesthesogens, it follows that if the rates at which these substances are replaced are not identical, the concentrations of certain ones will be restored before those of others. If this is the case, the waning after-image of an achromatic $S_d$ will become colored, and may go through a series of changes in sensory hue. This is actually found to occur. The exact order of these colors will obviously be determined by the
relative rates of supply of the several aesthesogens via the pigmented epithelium (cf. page 163); this, being a crude physiological process, should be expected to vary with the state of the organism, and with other factors not intimately connected with the exact nature of the original light stimulus.\footnote{Cf. M. F. Washburn, and S. J. Franz. Bibliog. p. 404 f.}

The Luminosity of the After-Image

The explanation above offered to account for the production of negative after-images is not particularly novel. Helmholtz supposed the after-image to depend in just this way upon the subtraction of one component of the so-called proper light of the retina, the remaining components of course being complementary with respect to it. Ladd-Franklin, Hering and others have objected to this explanation on the ground that the "intensity" of the negative after-image is often as great—or even greater—than that of the original stimulated sensation, so that the negative after-image may, upon certain occasions be adequate to entirely neutralize the initial positive image. The enfeebled "proper light", it is claimed, cannot conceivably be so much more powerful than the unenfeebled "proper light" as to actually complement a stimulated sensory quality. Observation, it is affirmed, shows that the negative after image is often more luminous than the surrounding neutral gray; this fact is inconsistent with the theory that it has resulted from the subtraction of some element of this gray. This difficulty is a real one, but it can easily be met on the basis of our hypothesis. In studying the mechanism underlying simultaneous contrast, we have seen (page 380) that the stimulation of a certain retinal element \footnote{Cf. M. F. Washburn, and S. J. Franz. Bibliog. p. 404 f.} causes it to develop a negative electrical charge, and that consequently, not
only do the surplus negative ions produced in \( Z_{R'}d \) move away from this element, but positive ions from the outlying regions move towards, and into, it. As a result the concentrations of all of the molecular resonators except the one most powerfully acted upon by the light stimulus employed, will suffer an increase, and if the time of stimulation is sufficiently long there will also be a corresponding increase in the concentrations of the uninvolved aesthesogens. This effect may be sufficiently powerful to bring these concentrations to the point where the unstimulated ionizations are adequate to the complete complementation of the originally light stimulated reaction. Whatever may be the case, it is certain that the consequence of our postulates here emphasized cannot be avoided without some alteration in our fundamental hypothesis; the negative after image must be more luminous than an analyzed neutral gray. It is to be noted that the positive ions which move into \( Z_{R'}d \) will be determined in their quality by the nature of the positive ions existing in \( Z_{R'0} \), and that the ratio of the numbers of the various species undergoing this migration will be equal to that of the same species concentrated in this latter retinal element. This will also be the case in regard to ionic migration from \( Z_{R'd} \). If the resonator principally affected is \( M_r \), more \( I_{r-} \) ions will move away from \( Z_{R'd} \) than \( I_{r+} \) move towards it. But since the number of \( I_{r-} \) ions moving away from \( Z_{R'}d \) in the retina is equal to the number of \( I_{r+} \) ions departing via the optic nerve fibres, there must be an actual loss of \( M_r \) material, although the other—unstimulated resonators are gainers. It is to be noted, also, that the increase in the complementary ionic concentrations is
an increase in positive ions only, and that there must be a
loss of negative complementary ions from \( Z_{r'd} \) along with the
loss of \( I_r^- \) ions. Since the positive ions are those which con-
stitute the visual impulse, and since the impulse intensity de-
pends only upon the concentration of these ions, this decrement
in the concentrations \( i_g^- \), \( i_y^- \) and \( i_b \) in \( Z_{r'd} \) will not immediate-
ly interfere with the increased luminosity due to the contrast
migration. It will mean, however, that this increase will be
relatively short lived after \( L_d \) is removed, and that the phase
of brightness of the negative after image will be followed by a
phase of low luminosity. This effect is easily observable in
the waning of any powerful after-image. When the light
\( L_d \) is daylight and \( Z_{r'0} \) is unstimulated the achromatic contrast
effect discussed on page 378 will take place, so that ions of
all species will pile up in \( Z_{r'0} \), forcing back all of the four
normal ionizations in this element, and inducing a correspond-
ing blackness in the visual field at \( S_0 \). Upon taking away \( L_d \),
therefore, the stimulation process in \( Z_{r'0} \) will not only be
more intense than that occurring in \( Z_{r'd} \), but it will rise above
that normal to an un-light-stimulated retinal element. Conse-
quently the after image of \( E \) will be more luminous than the
neutral gray. A similar explanation accounts for the well-
known "corona of the after-image." Insufficient time makes
it impossible to develop the exact quantitative basis of the
reactions which we have outlined only qualitatively above; our
mathematical postulates make it perfectly possible to derive
quantitative expressions for all of these after image effects
which should be experimentally verifiable, in so far as such a
verification is consistent with the general metabolic instability
of living organisms.

The Positive After-Image.............. Although it will be somewhat out of place a word may be said here concerning the probable mechanism of the so-called positive after-image.

G. J. Burch, it will be recalled, noted that after prolonged intensive stimulation of the retina with a homogeneous light "a positive after effect remains as a luminous fog." It has been observed that, as a rule positive after images only appear with unusual stimulus intensity, and our explanation of this phenomenon will be that the effect of this undue influx of sensory ions at the cortical element over-taxes the chemical and physical mechanisms existing in this element for the elimination of the ions in question, so that the cortical dissipation constant is altered with respect to these ions. Suppose, for example, that excessive stimulation with \( L_{500} \) takes place; the cortical tissues will be flooded with \( I_{g^+} \) in such a degree that it will be impossible to for adequate removal of this substance to occur; the result is a green positive after image, or the green haze of Burch's experience, if the entire retina is affected. The purple after-image sometimes observed we regard as being due to the fluorescence of a partially decomposed visual purple, or more strictly to a phosphorescence similar in mechanism to that exhibited by the salts of quinine.¹

Course of the After Image of Brief Stimulation..... Concerning the origin of the "ghost" or "satellite" which follows the image of brief stimulation we accept the explanation of von Kries, viz., that this "ghost" is the delayed response of the achromatic visual system, the velocity of the impulse

u, (cf. page 266) in this primitive system being naturally smaller than that characteristic of the more modern chromatic system of the cones.
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PART TEN: THE EVOLUTION OF THE VISUAL MECHANISM.

Section XXXVI: The Biometrics of Visual Response.


In the study of any special biological structure, and the functions of this structure, one should not lose sight of the fundamental and general conceptions of biological science, whether these be empirical or hypothetical. There are two closely related points of view which it seems advisable to adopt in considering certain aspects of the problem upon the solution of which we are now engaged, because that problem—the nature of the visual mechanism—is one with respect to which no general biological principle can be irrelevant. These are the viewpoints of the theory of evolution and of the science of biometrics. In a certain light biometrics may be regarded as a mathematical investigation of the evidences for evolution, and since we believe that living forms, with all of their characteristics, are the products of an evolutionary process it is inevitable that in a detailed consideration of such a subject as visual sensitivity, we should make use of both evolutionary and biometric conceptions. The former are hypothetical—like our thesis—but they may be regarded—in part, at least—as interpretations of the latter, which are empirical, just as hypotheses of visual response may be regarded as interpretations of the empirical facts of that response. Let us first consider briefly the fundamental principles and general results of biometrics, in order that we
may understand their meaning in certain applications later to be made to the facts of visual response.

**Biological Species and Their Variations**

In science one always generalizes; one makes statements which are supposed to describe a large number of individual cases. Now in the non-biological branches of science, this process of generalization meets with no great difficulties, because the subject-matters which are considered are approximately constant in their characteristics, constant, often, beyond the capacity of our methods of measurement to detect variations. But in biology this is not the case. Here, as elsewhere, we indulge in generalizations, but we are forced to qualify these generalizations in a special manner. In physics and chemistry the emphasis is placed upon constants, but in biology one is forced primarily to emphasize the existence of variants. When we speak of a particular biological species we admit that the exemplars of this species are far from being identical, and that in certain cases the differences existing between them may be such that we are even uncertain whether they are actually members of the same group; but at the same time, it is clear that the species possesses a certain amount of reality, -- and it is the business of biometrics to determine the meaning of this apparent real specificity.

**The Biometric Method**

The biometrician begins by selecting at random a certain large number of representatives of what he believes to be a single species. Each one of these representatives he calls a variant. He next chooses some single character exhibited by the variants and subjects it to numerical measurement in each variate. This character may be such a one as length of arm or wing, color of hair, or--in our
problem—the nature of the visual response to definite homogeneous or heterogeneous lights. Having determined the degree in which each one of the variates exhibits this specific character, the biometrician divides the total number of variates—called the population—into classes which are defined in the following manner. The total range of the measurements of the character in question may be supposed to lie between the quantities A and Z. In this case the distance A--Z is divided into n equal parts, and the variates whose character measures fall within any one of these divisions are said to belong to the class which that particular division represents, and the number of variates falling within a certain class is known as the frequency of that particular class. Now if we represent the results of this process graphically, by plotting along the abscissa axis the magnitude of the classes A to Z, and along the ordinate axis the corresponding class frequencies, we obtain a curve which is characteristic of the species and species character measured, and which may be called the variability curve of the species. These curves are more or less similar for all species and all characters; they closely resemble that commonly known as the curve of error. This latter curve is symmetrical, rising to a single maximum at a definite point, and sinking on either side of the maximum so as to become zero only at infinity. Now in the biometric instance the class (abscissa) corresponding with the maximum is known as the mode of the curve, and the corresponding organic form is called the type. The typical character in biology is thus that character having dimensions such that the average of all other homologous characters in the species considered vary from it the less
the more are taken at once. Now it sometimes happens that when the biometrician follows the above procedure, selecting his variates at random and measuring and plotting the magnitudes of certain of their characters in the biometric way, he obtains curves having two or more modes, and which thus present two or more typical forms. In this event he is usually persuaded that he has made an error in the selection of his variates and that the number which he has studied contain representatives of more than one species. But it is clear that this simply amounts in the last analysis to a definition of a species as the sum of those biologic forms falling within a certain region on either side of a certain type form, and not including any other type form or its proper variates. In order to avoid possible confusion, we shall call a species thus defined a germinal species, and the meaning of this denotation we shall now attempt to make clear.

The Hypothetical Basis of A Germinal Species. "There is an hypothesis which serves as a physical interpretation of the facts deduced by biometrics. The tendency in modern biological thinking is to regard all of the native characters of an organism as the expression of the constitution of the germ from which this organism sprang. The line of investigation which is known as Mendelian has shown that many of the attributes which serve to distinguish varieties and species can be considered as unit characters, which in experiments on interbreeding are found to be either present or absent, and not to melt into each other. The inference is that these unit character depend upon unit elements of the germ plans,—in the language of Weismann's hypothesis, up-
on specific biophores. The members of any single species in the biometric sense may be regarded as the offspring of a common ancestor, and should therefore be developed from the same germ plasm. We might expect such offspring to be identical, but if we consider the fact that the so-called continuity of the germ plasm is not an actual continuity but merely a process in which one germ-cell gives rise without intermediate processes to another germ-cell, we can see that on account of the molecular factors involved in this reproduction, the reproduction itself may not be exact in each and every case; in reproducing itself the germ plasm should be expected to make errors, and these, of course, ought to follow the law of error, and as a result the many offspring from a common stock should vary from the stock itself by a greater or less amount according as the variation in the germinal elements was greater or less. But since we expect more slight errors of reproduction than great ones, the variability curve of the organic character determined by the variant germinal element should be that of error, and the mode should represent the original stock itself. The variation of a single biophore could produce but a single mode. But we have said that the biometrician often develops curves having more than one mode. When he obtains results of this sort he usually comes to the conclusion that the variation which he has been studying are not those dependent upon the mutations of a single underlying element in the germ plasm, but depend, rather, upon the variation of two independent germinal elements. As a rule this leads him to divide the variants into two species or varieties, as we have noted.

Species and Varieties of Visual Response

It is obvious that the problem which we have been considering
in the present thesis must be defined as the description of the typical mechanism of visual sensitivity, and thus we have been mainly concerned with that form of visual response which is commonest in the human organism and consciousness. Biometrics shows us that in studying any biological structure or process such as those underlying visual sensation it is reasonable to suppose that in the examination of many examples of the phenomena in question we shall discover that they all hover more or less closely about a typical form, but that, on the other hand, it would be contrary to the general principles of biological science to suppose that the phenomena and hence the hypothetical underlying structures, of visual sensitivity will be quite constant as we vary the individual studied, and that it would also be unreasonable to deny that an occasional extreme divergence from the type may appear. Radically atypical forms of this character must, however, lie upon that variability curve the mode of which determines the type. If we find that this is not the case and that they are distributed in classes in such a way as to yield a new maximum in the curve, and thus a second or a third -- mode, we must define a new type and infer that the underlying germinal elements are specifically different in kind from those of the species determined by the primary type.

A Method For Determining... It is conceivable, upon the the Number of Germinal basis of the fundamental assump- Species of Visual Response tion of psycho-physical parallel- ism (cf. page 113), that one might be able to make a biometric study of the visual sensation itself. If it were possible for us to determine quantitatively the degree in which the various attributes of the elementary visual sensation were presented in
the consciousnesses of a large number of observers placed under uniform stimulus, we might draw a variability curve in which the variant character was the elementary sensation. Something of this sort may be done even as it is, but more definitely satisfactory results can be obtained by a method which is more purely physical. This consists in an application of the so-called device of color mixture. One of the interesting features of the psycho-physics of visual response is—as we have previously noted—the fact that when the same area of the retina is stimulated by the use of a heterogeneous light the colors (hues) normally induced by the component rays of this light do not appear, but in their place there is presented another hue which may or may not be that corresponding with some homogeneous light. In case it is possible to find a homogeneous light inducing the same sensory hue this may be thrown upon an adjacent portion of the retina and the conscious effects directly compared. Now suppose that an experimenter, E, selects two different homogeneous lights, $L_1$ and $L_2$, which he throws upon adjacent areas of the retina of an observer, O, the intensity of these lights being kept constant. E now mixes with $L_2$ a third homogeneous light, $L_3$, so chosen that by varying its intensity the sensory hue induced by the heterogeneous light ($L_2 + L_3$) can be made the same as that induced by the adjacent homogeneous light, $L_1$. E now requires O to report when a true match is obtained, and he records the intensity, $e$, of $L_3$ demanded in fulfilling this requirement. If the observer now be changed it will be found that the $e$ of $L_3$ required for a match by the second O will be somewhat different from that demanded by the first O. After making measurements upon a large number of observers in this way it becomes
possible for $E$ to construct a variability curve in which the variates, $0$'s, are classified in accordance with the intensity, $e$, of the light, $L_3$, required to produce a match. If among these variates there is but a single germinal species the resulting curve should exhibit but a single mode. If, on the other hand, a number of well defined maxima occur, it will be quite necessary to decide that the germinal species are manifold.

The Five Types of Visual Response. Now as a matter of fact the biometric study of visual response by the use of a method similar to but more elaborate than that above described shows that there are at least five distinct maxima in the variation curve for this response. In making this statement we do not wish to imply that any systematic attempt has yet been made to apply the conceptions of biometrics to this particular problem, but merely to indicate that from the data now extant, and gathered largely for other purposes, this conclusion may be safely drawn. The limitations of this thesis have not permitted the collation and analysis of all of these data, but in the accompanying Fig. 15 we have plotted the results of some measurements of von Kries, so as to show that out of twenty cases of so-called dichromatic vision two widely separated types appear. It is found that when the retinas of a large number of subjects are stimulated with a heterogeneous light composed of two homogeneous lights of known frequency the majority of the subjects report that the sensory effect is the same as that corresponding with a certain other and different homogeneous light. The "matches" vary somewhat for the eyes of these observers, but the variations are of such a character as to conform with biometric expectations.
based upon belief in such a unity of species. In other words the comparative study of workings of a large number of visual mechanisms reveals the fact that these mechanisms fall into groups which must be adjudged distinct germinal species, because they are biometrically separate; they must depend upon distinctly different germinal architectures.

Basis of a Complete Biometric Analysis of Visual Response............. The five types which we have asserted are revealed by the biometric study of visual response do not appear in matching experiments in which only two definite lights are mixed, the induced sensation being compared with that induced by a third definite light. The use of three pure components is necessary in the formation of the heterogeneous light, all of which can be varied in intensity and it is found that with different intensities of these three lights all of the sensory hues inducible by homogeneous lights can be matched. Thus, if the three components of the heterogeneous light are \( L_1, L_2 \) and \( L_3 \), and their respective intensities are \( e_1, e_2 \) and \( e_3 \), by varying the ratio: \( e_1 : e_2 : e_3 \), the sensation, \( S_{ht} \) induced in the visual field by the heterogeneous light may be made chromatically the same as the sensation \( S_{hm} \) which is induced by any homogeneous light \( L \). When \( L \) is varied so as to include practically the whole spectrum and \( e_1, e_2, \) and \( e_3 \) are adjusted for matches, values of these latter variables are obtained which completely characterize the particular observer concerned. A large amount of data of this sort derived from the examination of many observers should permit the experimenter to make variability curves which will reveal all possible deviations from singleness of type.
Fig. 15.

BIOMETRIC PLOT SHOWING THE DISTRIBUTION OF TWENTY CASES OF
"DICHROMATIC" VISUAL RESPONSE.

Ordinates: Class Frequency.

Abcissae: Intensity of Light from the Lithium Line Required
to Match a Given Intensity of Light from the Sodium (D) Line. Arbitrary Units.

Data from:

KRIES, JOHANNES von: "Uber Farbensysteme; (1897); Zeits.
259.

2. LUCKEY, G. W. A.: Comparative Observations on Indirect Color Range; (1895); Amer. Journ. of Psych., vol. 6, pp. 439-504.

3. MAGNUS, H.: Untersuchungen über den Farbensinn der Naturvölker; (1890); Jena.

4. RIVERS, W. H. R.: (On the Color Sense of Aborigines); (1901); Pop. Sci. Month., 1901, p. 44.


We have indicated that in all probability a thorough biometric study of visual response would reveal the presence of at least five distinct types. Now there are two ways in which the existence of five different germinal species of *Homo sapiens* with respect to the character of visual response can be accounted for. In the first place we might assume that these five specific forms are quite without relationship with each other, representing entirely different lines of development of the visual mechanism; or, second, we might suppose that the visual mechanism which is typical of *Homo sapiens* as a whole is dependent upon the existence in the human germ of a complex of germinal units, and that five different species of visual response are the outcome of the absence of one or more of these units.

The Heredity of Anormal Types. An examination of the genetic relationships of specific variates in the divers species makes it possible to assert that the latter explanation is the only one which can be accepted. By far the greater number of variates fall into a single species, the type corresponding with which we call the normal type. The other four types will be spoken of as anormal types. Now the study of the heredity of variates belonging to anormal species shows that, while there is a tendency for the species to perpetuate itself, these anormal variates do not belong to a pure generic line all of the members of which exhibit the characteristic response in question, but, instead, are anomalous members of a line the greater part of which
represents the normal type as regards visual response. It is apparent, then, that the anormal variates are atavistic in their character; their genetic constitution is a reversion to types now for the most part superseded.

A Possible Complexity of Lineage in Visual Response

Now it is possible to assume that these archaic types have no relation—other than that of competition—with the modern type. According to this view, at least five species of *Homo sapiens*—or its precursors—must have at one time existed; these species were different with respect to their visual, but, by interbreeding, the five distinct germinal visual elements were placed in competition, the result of this competition being the victory of a single element, that which we have called the normal. The appearance of anormal types at the present stage of evolution must depend upon occasional failures of the normal germinal visual element to dominate in the germinal architecture, the usually recessive archaic anormal elements slipping in instead. This view, which is the only possible evolutionary basis of a theory of the independent character of the five visual types, necessitates a conception of the line of development of the human species as a whole which cannot be accepted. Although the human visual mechanism is, in all probability, much older than the race itself—W. E. Gladstone and his followers to the contrary notwithstanding—1—we have no reason for believing that it depends upon any such complex origin as the one above sketched. A much more probable view is the following.

1 See GLADSTONE, W. E.: The Colour-sense; (1877); Nineteenth Cent., year 1877, pp. 366-388. Also LUBBOCK, SIR J.: On the Development of the Colour-sense; (1882); ibid., vol. 37, pp. 518-529, and other references in Bibliography, page 444.
The Building of the Visual Determinant.

In the course of the phylogenetic development of any organ (and function) there must be an increase in the complexity of the germinal unit corresponding to that organ. In the beginning a single biophore may have sufficed, but as the organism grows more complex the number of determining biophores must increase. A highly differentiated apparatus—like that underlying visual response—must be represented in the germ plasm by a mosaic of elements. Now certain groupings of these elements will correspond to progressive stages of development of the organ in time, and in the process of reversion should be expected to occasionally recur. It is clear that if the mosaic is represented by the elements ABCDE, and the development be supposed to have taken place in alphabetical order, these successive groupings will be: 00000, 00000, 00000, 00000, 00000. In the normal type of vision we may suppose the germinal architecture to be represented by the last group. This grouping, then, will be dominant in all normal varieties, while the remaining groupings will be normally recessive. However, we should expect to find an occasional regression to the grouping ABCD, a less occasional reversion to ABC, etc., in accordance with the law that the frequency of reappearance of an ancestral trait is inversely proportional to its antiquity. We can, then, explain the existence of five distinct types of visual response upon the assumption that the underlying germinal determinant of the normal type is complex, and has been developed phylogenetically by a successive addition of new biophores.

The Complexity of the Developed Visual Mechanism

But a complexity of the germ demands a parallel com-

1 See. WEISMANN, A.: The Germ Plasm.
plexity of the organism. If the determinant of the normal visual mechanism is complicated in structure the mechanism itself must be complicated in a parallel manner. And if the germinal determinant of the anormal type can be regarded simply as a particular stage of reduction or development of the normal, then the corresponding anormal mechanism must be regarded as bearing a like relationship with the normal mechanism. On the basis of this genetic argument alone, then, we should expect to find physical and psycho-physical evidence that the different species of visual response can be arranged in a series so that in passing from one member of the series to the next the change observed is simply one in complexity. Something of this sort may actually be accomplished.

The five types of visual response which we have considered above as characterizing the biometrics of this particular field of investigation must be regarded as partly symbolical in their nature and meaning. The actual situation is much more complex than this preliminary argument might lead one to suppose. At a later point in our thesis we shall consider it somewhat more in detail.
Section XXXVII: A Descriptive Outline of the Probable

Phylogenetic History of the Visual Mechanism.

Chapter 25: The Methods and Advantages of Evolutionary Discussion With Reference to the Problem of the Nature of the Visual Mechanism.

The Final Justification of Hypotheses... In the attempt to imagine a hypothetical mechanism which will serve to explain all of the facts of visual response one is led to postulate the physical existence of structures possessing a considerable degree of complexity. From the standpoint of general utility, and hence from the standpoint of acceptability and ease of defence, complexity in hypothesis is unfortunate; it often arouses the impression, if not the assertion, that the hypothesis in question is probably physically untrue, and that the finally valid conception of the underlying factors concerned will be at once simpler and more in harmony with the facts. Often such a criticism is correct, but in the field of biology one cannot be sure that complexity alone may with justice be regarded as an indication of the non-finality of an hypothesis, for the empirical, quite unspeculative investigation of biological processes and structures reveals the indubitable existence of very intricate relationships throughout the biological world. In the foregoing pages of this thesis we have postulated the existence, in the brain and retina, of certain physiological mechanisms which at the time of their postulation may have seemed gratuitously assumed. One may be inclined to say that the adoption of assumptions in such a way as this is justified if the assumptions in question harmonize with
the experimental facts of the department of nature to which they are referred. This is indeed an adequate justification in physics and chemistry, provided it can be shown that no other hypotheses than those brought forward can be in better harmony with the facts. But in biological speculation, there is another—an a more final—type of justification which can be sought for the acceptance of specific hypotheses, and that is the proof of the harmony of the hypotheses with the evolutionary theory of organic origins. It remains for us to show that the hypothetical mechanisms the existence of which we have postulated are such as may conceivably have developed in accordance with the methods and processes of organic evolution.

Fundamental Evolutionary Requirements

The fundamental requirement imposed by the theory of evolution upon all biological structures and functions, whether factual or hypothetical, is that of the possession of survival value. We cannot legitimately postulate the existence of any mechanism which we cannot show to be of utility to the organism of which it is supposed to be a part. Taking into consideration the conditions presented in the form of physical and chemical laws and elements, it must be admitted that the development of organic structures by a gradual evolution from the simple to the complex will yield structures subserving the purposes in question in the simplest manner. Every complexity must be justified by a demonstration of its physical necessity in the meeting of the circumstances in which the organism is placed, or by a proof that it is a consequence of such an adaptation in combination with pre-existent and more general laws, such as those of physics and chemistry.
The above principles apply, of course, only to established organic characters, and not to such attributes of individual members of a species as may be considered unique chance variations from the type founded in the germ plasm characteristic of the species. In addition to the above fundamental requirements of evolutionary theory, it is necessary that one be able to give a reasonable historical account of the path of development followed in the production of any postulated mechanism.
Chapter 26: A Preliminary Sketch of the Course of the Evolutionary Development of the Visual Mechanism.

The Origin of the Achromatic Visual System

Geology and the theory of planetary evolution assure us that during that period of the earth's history in which organic forms first arose and during which they passed through their preliminary course of development, the terrestrial globe was enveloped in a heavy cloak of water laden air through which the rays of the sun penetrated with great difficulty. According to Professor Lowell the landscape and sea-scape of Carboniferous and pre-Carboniferous times was almost wholly a chiaroscuro; the vegetation was cryptogamic in habit, the sky was a uniform dull gray of cloud, and all things were shrouded with haze. The earth was done in monochrome. Organisms developing in such circumstances would profit by vision, but by vision of a special kind, namely one which could occur efficiently with a low intensity of illumination, and which took no account of homogeneous lights,—because none were present. We should expect, in accordance with the evolutionary view, to find that the visual apparatus of the early animals was such as to permit a differentiation between various shades of gray—that is, various intensities of a practically uniform mixture of wave-lengths—with a general very feeble illumination, but not that there would be perception of color—the differentiation of wave-lengths. On account of the haziness of these early atmospheres capacity for delicacy of discrimination with reference to outlines and details would also be unnecessary, and hence the nervous connections and elements would be rougher than as if more definite images of objects were possible. Paleontological
LOWELL, PERCIVAL: The Evolution of Worlds.
evidence seems to indicate that the earliest fishes were blind; there was in all probability practically no light at all even a short distance below the surface of the primal seas. But as oceanic forms crept or were cast ashore, and as the skies gradually brightened, visual mechanisms began to be possible. It is clear that the retinal rods, found as constituents of the optical apparatus of organic forms to-day, are the heritage of the modern types from their early ancestors, -- for the rods are not only mediators of the images of the dusk, and incapable of wave-length discrimination, but are also, by reason of their bluntness and their multiple neuronic connections, less adapted to delicacy in space perception than the cones.

The Origin of the Retinal Cones... We have reason for believing that the period of primitive night upon earth was very protracted indeed, lasting many millions of years, but finally the clouds broke, and the sunlight shone for the first time for living creatures. This event was a critical one; it brought new evolutionary forces into action, forces by virtue of which certain organic forms were destined to advance in differentiation, while others perished or fell in position and power. A blind animal is practically at the mercy of one which is capable of vision; and in the struggle for existence against natural forces the odds are immensely in favor of the latter. When the sunlight came the intensity of its energy destroyed those chemical substances which were present in the rods of the primitive retina and upon the reactions of which the sight of the primordial animals depended, -- so that they became blind once more. Three alternatives were thus presented, between which the zoological forms competing in the
struggle for existence might choose. First, they might perish on account of their blindness. Secondly, they might adapt themselves to nocturnal life. Or, third, they might develop new visual elements capable of dealing with the novel brilliancy of pure sunlight. As a matter of fact probably all of these processes occurred. Many animal types disappeared altogether under the stress of the new conditions. Others, whose memory is perpetuated by the owls, bats, and similar nocturnal species, were able to fit themselves for activity at night. These must have been flying or burrowing organisms capable of selecting a place of comparative safety for the inactivity of the day. But still other species grappled with the situation and produced new variations in visual mechanism, which permitted daylight seeing. That these variations, after selection, should prove to be additions to the primitive structures, rather than replacements of them, is explained by the fact that owing to the rotation of the earth, the hours of darkness did not entirely vanish with the coming of the sunlight, so that dark-adaptation was still a desirability, and the loss of it would bode ill to an organism. The new visual elements were the cones, and since clear skies were accompanied by an introduction of color into terrestrial vistas—the presence in the retinal image of areas of relatively homogeneous light—the appearance of phanerogamic plants with their outburst of blossoms, and the dissipation of the gray mist, it became advantageous for animals to react with reference to light-waves of different lengths in a specific manner. Hence we should expect the new retinal elements, the cones, to mediate color sensations. Similarly, on account of the increased definiteness of images, they
should permit sharper perception, and hence must be more delicate in structure, and must have finer and more specific connections with the center or with the motor apparatus. Both of these expectations are fulfilled, if we regard the cones of the retinas of present day vertebrates as the existing expression of the process of evolution which has been outlined.

Further Differentiation of the Eye.........

The development of the eye as a camera must have paralleled this evolution of the retinal structure, but since in this thesis we are not concerned with the more purely optical aspects of the visual process, this accessory factor in the process of differentiation may be neglected. It may be noted, however, that, regarded simply as an optical instrument, the eye is a very inferior piece of apparatus even at its present highest stage of perfection. During earlier times the efficiency of the lens system must have still smaller. Taking into consideration, therefore, the well-known facts that crude lenses give distinct images only in the centers of the fields, we might predict that in the struggle for existence between animal species for the advantages entailed by increased fineness of perception, the retinal elements capable, by virtue of their peculiar structure and connections, of mediating that delicacy of discrimination, would crowd to the region of maximal efficiency of the lens, and at this point, if not elsewhere, would replace the earlier and cruder structures. Thus we have the fovea, made up exclusively of cones, packed very closely together, and with a clear path for the best image the little camera can form. The function of the black pigment cells has already been made clear (page 163) and their evolutionary origin must have been of the simplest sort.

The Retinal Cells are Epithelial...

A single retinal cone-cell is morphologically similar to the cells which constitute columnar epithelium, and phylogenetic—as well as ontogenetic—considerations lead us to believe that they are, in fact, differentiated epithelial components; the retina is a specialized epithelium. In sponges and medusae we find certain cells, hardly distinguishable in form from the remaining elements of the outer tissues, which are sensory in function, and these cells show marked resemblance to the cone and rod cells of the retina, although they are not, of course, obviously or actually so highly differentiated. We may suppose, then, that the primitive retina was formed by a specialization of epithelial tissue, first in the line of general increased sensibility to stimulation, and second in the development of a particular sensitivity to light.

The Function of Pigments in the Development of the Retina.................

A. Pizon has well pointed out that the origin of the light sensitive retina is in all probability bound up with the accidental pigment excretion which occurs normally at certain points upon the surface of the organism. Primitive visual organs—whether phylogenetic or ontogenetic—are usually simple "pigment spots." In the first instance this pigmentary material is simply a metabolic waste product which is brought to the surface of the body for purposes of elimination. But a pigment is, physically, merely an absorber of light energy, and it

follows that wherever pigment is segregated there conditions are ripe for the development of a light sensitivity. A primitive pigment spot is a collection of a great variety of pigments; amongst these there will be certain ones which absorb light energy with the production of chemical change, undergoing the type of photo-electrolytic dissociation which we have already described in much detail (cf. page 177). No assumption is involved in supposing that such light sensitive bodies will be present in the aboriginal cuticular pigment spot; it would be an assumption—and an unjustifiable one—to suppose that they were not present.

We shall not here attempt to defend The Primitive Visual Neurosis............. the doctrine which we have advanced with reference to the nature of the nerve impulse, by an appeal to evolutionary conceptions, since there is insufficient time at our disposal. Assuming that it is possible to provide such an evolutionary justification of the idea that the nerve impulse—even the primitive nerve impulse—consists in an active absorption and transmission of the stimulating chemical substance, or of some chemical substance released by the stimulus, in the form of ions, we may endeavor to sketch the course of development leading to the peculiar visual nervous mechanism described in Part Eight.

In all probability the olfactory sensory system may be correctly regarded as presenting the most primitive type of organization of its kind to be found in the vertebrate organism. In this system all—or almost all—of the ions presented to the neuro-fibrillar transmitters (cf. page 238) are transmitted to the centers. In the beginning the visual nerves must have been of this character;
almost any positive ion which came into contact with the nerve endings would be transported to the brain. As we have noted above the genesis of the visual ions in the primitive end organ is to be assigned to the collection at that point of a large concentration of pigmentary material. This material is intrinsically light sensitive. Now it is likely that the pigment which was present in the aboriginal eye-spot was far from being a chemically pure substance; it must have been made up of a large number of bodies capable of a selective absorption of light, some of which were acted upon by the absorbed energy in such a way as to bring about decomposition in the form of increased ionic dissociation. The original visual nerve fibres—which were simply fibres of the ordinary free-end olfactory type—would thus have been excited by a great variety of visual ions, and the quality of the visual impulse at the brain would have been very complex.

The Function of the Cortical Luminosity Element...........

Under such conditions it would obviously be very desirable in the first instance that this qualitative complexity be simplified in such a way that a cerebral state or process varying only quantitatively could be established upon the basis of the impulse as it was presented. Since it is difficult to conceive of the translation of a multitude of chemically different substances into a single unitary substance by a chemical reaction process it seems likely that the means employed to reduce the qualitative manifold will be physical in nature, depending upon some common quality possessed by all of the components of the impulse. Now the most obvious common property of the ions is their ionicity, i.e., their common possession of an electrical charge. Let us suppose, then,
that a mechanism arises in the cortex by the functioning of which an effect is produced which is proportional merely to the degree of positivity of the afferent ionic mass. The nature of this mechanism may be very readily figured. Imagine two adjacent neurons one of which is in direct neural connection with the end organ, and the other of which is the neuron which is to be included in the visual synergy (cf. page 257). The two neurons thus postulated are separated by a membrane—or an equivalent nervous connection—which is permeable to the negative but not to the positive ions, and we will suppose that in the neuron of the visual synergy is to be found a definite ionized substance having large positive ions and very small negative ions. In this case whenever the retinally—or pigment-spot—connected neuron is charged with positive ions from the impulse—no matter of what variety—the negative ions of the synergic neuron will move through the membrane under the influence of the negative potential gradient which is established. The synergic neuron will thus be left with an excess of positive ions, and is obviously the luminosity element of our hypothesis (cf. page 260) the retinally connected cell being the cortical receiver. It is not unreason able to suppose that the mechanism above described should arise as the result of accidental variation in the exact properties and interconnections of the cortical nerve cells, and once this variation occurred it would, if our analysis of the requirements of the situation is correct, be fixed by the action of selection, for it provides a means whereby the brain can unify and base efferent impulses upon the complex contents of the visual neurosis. The impossibility of the cerebral utilization of a complicated and inconstant afferent impulse by direct neural conduction is apparent in the light of our fundamental
conception of the general chemical basis of nervous reactions. (cf. page 244)

The Purely Actional Significance of All of the Aspects of Visual Response.....................

In evolutionary discussion the elementary sensation, $S$, with all of its attributes must be regarded merely as a symbol of $C$, and the differentiation of $C$ must be held to have some meaning in action, i.e., to exist only because it is the indispensable basis of some characteristic efferent nerve current. The only process by which the visual mechanism could have become differentiated is that of adaptation of the nervous organism to its environment. Every specific sensibility of the visual mechanism must have a specific motor or secretion- al significance. This must be true of those attributes of the cortical process which are paralleled by $W$, $B$ and the hues, as well as of the retinal structures and processes which functionally precede them. The value of retinal differentiation to a developing species lies entirely in the fact that it permits a more accurate adjustment of the organism to its environment, and hence an increase in the chances of survival and of reproduction. The central mechanism is simply a device for connecting the processes of the retina, in their most delicate discriminations, with special and maximally appropriate motor reactions. The development of such a central mechanism is a matter of the variation and selection of schemes of connection between the retinal elements on the one hand, and the muscular or glandular elements on the other. The successful schemes are represented by very complex systems of lines and relays, radiating from a sort of automatic switch-board, the central cortex (etc.). It is entirely a surprise to the physical
thinker, when he finds correlated with the machine-like workings of this great filar center the facts of consciousness.

The Effect of the Tendency of Neural Energies to be Conservative.......................... There are empirical and theoretical reason for believing that the energy of primitive neural elements is conservative, i.e., that if a certain stimulus is applied to the element it will be excited in proportion (logarithmically) to the energy of the stimulus, but that if a stimulus is removed it will become quiescent; nerve tissue normally borrows its energy from external sources; it does not ordinarily act when unacted upon. Hence we may say that except in some very special mechanisms the nervous energy which is employed in efferent (motor) impulses is that derived from afferent (sensory) impulses; the brain does not (like to) produce its own power; it simply directs that which is brought to it from the sense organs. In the absence of all stimulation of the sensory system, then, there should be a corresponding absence of motor impulses, if the nervous mechanism concerned is of the simplest type, viz., that founded upon the reflex arc.

The Antagonism of Differ-ent Motor Tendencies..... We have noted above the principle that every differentiation of the nervous system which occurs in the course of phylogeny can survive only in so far as it becomes the basis of some special type of motor response on the part of the organism. Now since at any stage in the evolutionary process the organism must possess some type of reaction to every stimulus, every nervous differentiation which occurs must involve a displacement of the exact type of reaction which obtained previously to its advent. The
new and the old reaction tendencies—if both remain—are therefore antagonistic; either one or the other must predominate, not both simultaneously.

The Effect of Clear Skies Upon the Development of the Visual Apparatus.... With the coming of clear skies in the Mesozoic world the signal was given for the development of those special light sensitive, light selective, mechanisms which mediate the sensation hues. It was necessary that animals living in the gloom of early geologic periods should avail themselves of every possible energetic source of information concerning their environment. The light response of the primitive luminosity system was based upon the photo-ionic sensitivity of a large number of pigmentation substances; this being the case the response would have been gross in character, that is to say, dissociation would have depended upon the relative energies of the light waves, rather than upon their periods of oscillation, at least within comparatively wide limits. Selective mechanisms are wasteful, but with sunlight and later exigencies of the struggle for existence, selective mechanisms had to come. The primitive chemical basis of these may readily be indicated. The disappearance of the primordial fog from the earth’s surface made possible the formation of optical images which were differentiated with respect to the homogeneity and relative wave-lengths of the light rays involved. Such a stimulation of the primitive retina with relatively homogeneous lights must have resulted in an increase in the concentration of certain visual ions in the cortical receiving cell, accompanied by a concomitant decrease in the concentration of certain others. Since these changes were not accidental but were directly related with the character
of the organism's immediate environment, they could usefully be
made the basis of differential reactions of the organism with
respect to that environment, --given the appropriate mechanism.
Now suppose that a special cortical cell develops which is capa-
bile of selecting one of the ions whose concentration is thus made
to depend upon the physical "color" of external objects, so that
changes in the cortical concentration of the ion in question may
be made the basis of a specific and appropriate motor reaction,
say--for example--that of moving away from the object or the con-
ditions producing the peculiarity of the stimulus. In accordance
with the principle of the conservation of nervous energies, the
tendency towards this reaction could result only from an increase
of the cerebrosis intensity within this cell, and if this in-
tensity should become zero there would not necessarily develop
a tendency to react oppositely--to approach the cause of the stimu-
lus peculiarity--, but merely the absence of any tendency to act
at all. However, no matter how an organism reacts, it is always
possible for it to react oppositely, -- that is, in some manner
inconsistent with, not capable of co-existence with, the original
reaction. This we have indicated in discussing the principle of
the antagonism of different motor tendencies. As a matter of
fact most vital organic activities are such as to permit arrange-
ment in opposed pairs, in just the fashion suggested; the most
fundamental of these are, of course, the opposed reactions of
approach and retreat. In very few situations is it desirable
that the organism should execute no adaptive action whatsoever;
if there is one possible type of movement or inhibition or physio-
logical adjustment which is distinctly disadvantageous, there is
generally another which is positively advantageous. Now we have seen that an increase in the initial cerebral intensity of certain visual ions on condition of homogeneous light stimulation is accompanied by the decrease of the initial cerebral concentration (cf. page 263) of certain others. It is possible, then, for two opposed actions to be based upon these two reciprocally related ionic concentration. Suppose, for example, that a reaction of retreat is based upon one, and a reaction of approach upon the other. It may be advisable for the organism to approach a "green" object, but to flee from a "red" one. In this case the approach reaction can be set off by the excitation of a nerve cell capable of being selectively excited by $I_{g^+}$, the retreat reaction by one capable of selecting $I_{r^+}$. 

Evolutionary Explanation of Complementation......

It is perfectly clear that the foundation of specific types of reaction upon selective light discrimination would be of great advantage to an organism in the struggle for existence. It is equally obvious that whenever—as is usually the case—a specific reaction involves the harmonious adjustment of the entire organic mechanism, no two types of action can occur simultaneously. Hence, no matter what the reflexes founded upon "color" may be, when they are different and based upon different "colors" they will be antagonistic. If they are not different they cannot survive, because of their inutility. It seems likely that color-perception is a secondary sexual character, which in the development of the human species has been transformed—or, rather, adapted to other purposes. Just what the specific reflexes—whether or not psychic—were, we cannot say, but if we adopt the approach
-retreat—or chromotaxis—reactions suggested above as an adequate representation of the general character of these reflexes, we may argue as follows. The primitive visuo-motor system was exclusively a "luminosity" system, based upon an objective chiaroscuro. This aboriginal system must have been quite highly developed, and certainly became firmly founded in the germ-plasm of the species. When the chromatic elements appeared they not only came into neural conflict with each other, but they also had to compete with the very highly organized, well grounded, luminosity system. The organism possesses but a single efferent mechanism, and for the control of this single important organization of nerve lines and trunks a sharp struggle must have ensued between the luminosity and chromatic elements. The outcome of intra-organismal selection of these elements would obviously depend upon relative utilities; organisms possessing retinal and cerebral structures capable of generating efferent currents with respect to particular wave-lengths of light would—when the conditions were well defined—exhibit valuable powers of adaptation to environment. But suppose that simultaneous messages were received at the centers affirming the presence of two or more widely different wave-lengths; suppose that—to make use of our "chromotactic" instance—both $I_{g^+}$ and $I_{r^+}$ are present at a certain time in about equal intensities in the cortical receiving element so that both $Z_{cr}$ and $Z_{cg}$ (cf. page 261) are excited equivalently. In this case both the retreat and the approach reactions would be set off, but neither could actually occur. If the two cerebrosis intensities were not quite equivalent one of the reaction tendencies would be dominant, but it would be much hindered in its predominancy by the activity of the opposite ten-
dency. It is obvious that this interference of tendencies would prove highly dangerous to the organism in which it took place, and, hence, that a device for removing one of the tendencies or both, so as to permit the functioning of the original very serviceable luminosity mechanism would be a distinct adaptation. It happens that this device is not at all difficult to realize, for it consists in the simple production of an amboceptor capable of removing the quarrelsome ions in exactly the same fashion in which other undesirable chemical substances are eliminated from the tissues. This is our evolutionary explanation of the existence of the mechanism of complementation which we have described on page 270 ff. This chemical artifice may be regarded as a scheme whereby the visuo-motor system is permitted to fall back upon its original discrimination machinery. The equivocality of chromatic discriminations often make them less available as a basis of action than the older method of discriminating relative light energies. It is freely admitted that this explanation of the peculiar fact of complementation depends for its validity upon the tenability of the postulate that the reflexes—whether essentially cortical or directly motor—founded upon the ions $I_{r+}$ and $I_{g+}$, and the ions $I_{y+}$ and $I_{b+}$ were distinct and antagonistic within each pair. The exact nature of these reflexes we have not attempted to conjecture. There is small doubt that they are at present, in the human species, at least, in a wholly vestigial state, -- but the suggestion may be made that the reflexes in question were such as to be psychically paralleled by desire and repulsion in each pair of complementaries and that in the so-called Gefühlsbetonung of the hues we have a the psychical representation of the vestigial motor tendencies.
themselves. As above suggested, the fact that color-blindness is a relatively sex-limited character (being forty times more common in males than in females) is in harmony with the idea that these emotional tinges of the colors are vestiges of erotic impulses, and their reciprocals. The subjective color-perceiving capacity of the female of the human species should be regarded in the light of the fact of the objective coloration of the males of lower species in the line of descent.

The Development of the Retina........ Parallel with this development of the cortical mechanism of vision, but largely subsequent to it, there must have occurred a refinement and differentiation of the retinal apparatus. In a previous chapter (page 426) we have outlined the plan of the histological development, the differentiation of the rods to form the cones, etc. A word may be said here concerning the more fundamental chemical differentiation. We have imagined that in the first place there existed in the retinal pigment cells a large number of pigments, some of which were chemically light sensitive. Originally all of these were involved in the visual impulse. But some of these pigments must have been more sensitive and hence more useful than others, so that as time went on a gradual elimination of the relatively insensitive substances must have taken place, their function being fulfilled by an increased number of the more highly sensitive ones. There would be a tendency for natural selection to eliminate from the retinal collection of pigments all but that particular pigment possessing the greatest light sensitivity, and with a maximum resonance at a point nearest that of the rays preponderant in the light which must be em-
ployed by the organism in its visual responses. On the other hand, since this light was in all probability of many wave-lengths a collection of sensitive substances responding to different frequencies of vibration might prove of superior value. It is not likely that either the visual purple, which we would naturally be led to suppose to be the original "luminosity" resonator, or the present day, human, chromatic resonators are identical chemically or genetically with the original pigments. In the course of millions of years of development, other and better light-sensitive bodies must have taken the places of the primitive ones. No doubt the visual purple, $\lambda_w$, is closely similar in its properties to the fundamental pigment of the Paleozoic retina, on account of its very high light-sensitivity. Among the chromatic elements we should expect those possessing the rarest qualities to be the latest in origin. Although the fundamental chromatic mechanism is probably very old it does not follow that all of the at present functional resonators are equally antique, or, at least, that they are still older, as our line of argument might suggest. It is perfectly possible—indeed wholly probable—that improvements have been made in the chemistry as in the histology of the retina since primordial times. Undoubtedly the rarest type of light-sensitive substance is one responding strongly to the longer wave-lengths; the maximum of actinicity in the spectrum is beyond the violet. Hence we ought to expect to find indications that the present $\xi_r$ is a fairly late evolutionary product. There are probably more feebly light-sensitive pigments than powerfully sensitive ones, and for this reason we should anticipate high sensitivity in the latest resonators, low sensi-
tivity in the earlier ones. In our hypothesis we have postulated a large $q_r$ and $q_g$, but relatively small $q_y$ and $q_b$. This means that $M_r$ and $M_g$ are modern productions, while $M_y$ and $M_b$ are older. This result is in harmony with the statistics of color-blindness (cf. page 455) and with the campimetrical distribution of the hues in normal vision.

Since we have found reason for believing that the cortical elements, $Z_{cr}$ and $Z_{cg}$ are correlated as parts of a balanced actional mechanism. $Z_{cy}$ and $Z_{cb}$ are connected in the same way. Since these pairs of cortical chromatic elements are phylogenetically related they are also in all probability also ontogenetically related, so that we should expect to find evidence that $Z_{cr}$ and $Z_{cg}$ are dependent in individual development upon a single germinal determinant, and that $Z_{cy}$ and $Z_{cb}$ are expressions of a second and distinct determinant. Let us call these determinants $Z_{org}$ and $Z_{cyb}$ respectively. On the other hand, since the retina is anatomically--although not developmentally--separated from the visual cortex, it is reasonable to suppose that it is determined by separate germinal factors, and that the retinal resonators, for example, are not necessarily correlated biometrically or germinally, with the corresponding components of the cortex.

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Section XXXVIII: The Problem of Color-Blindness.


Specification of Anormal Visual Types............

In the first Section (pages 407 to 416) of this Part of our thesis we have affirmed the existence of at least five separate types of visual response, and we have shown by an actual diagram (page 416) how at least two of these types may be clearly demonstrated by biometric methods. It is now intended to consider somewhat more in detail the properties of the two types in question, and to ask in what way—if at all—a genetic explanation of the existence of these types (and others) can be developed in harmony with the line of thought suggested in Section XXXV, Chapter 24 and consonant also with our own or with extant hypotheses.

The predominant visual type is, of course, that one which we have termed the normal; it is the type in which stimulation of the retina with each of the spectral lights brings about the induction of a series of sensations exhibiting all four of the hues which we have described in our analysis of the elementary sensation.

The mechanism underlying this type is that designated by the German physiologists as a "normal trichromatic color-system," because three distinct lights must be used in mixture experiments in order that all of the spectral colors (sensory hues) should be matched in sensation. The anormal types are represented by the so-called forms of color-blindness, or of color inefficiency. Of these there are four which are well recognized. The commonest
form of all is that known as "red-blindness," Daltonism, protan-
opia, or scoterythrous visual response. In this type of vision
lights of the longer wave-lengths apparently fail to induce the
hue R, and in place of G, Y, B or W are said to be induced by the
corresponding lights of the physical spectrum, according to the
frequency of the light concerned. The most striking physical
peculiarity of this type is that embodied in the low stimulus value
of lights of low frequency. In matching tests in which the lights
whose induced sensations are compared are \( L_{ht} = L_{500} + L_{700} \) and
\( L_{hm} = L_{590} \), the scoterythrous type requires an intensity of \( L_{700} \)
which is five times as great as that required by the second anor-
mal type, the deuteranopes, so-called "green-blind," or photery-
throus variates. This is shown in our Fig. 15. The two other
well-recognized anormal visual species, needed in the perfection
of our symbolic five (cf. page 421), are the "blue-yellow blind",
and the totally color-blind. In addition to these there are other
anormal forms of visual response which are probably determined by
specific germinal architectures; amongst these the so-called
"anomalous trichromatic color-system" should be mentioned.

The Visible Spectrum as Described by a Scoterythrous Ob-
served by use of the entire physical

When the eye of a scotery-
spectrum (dispersed), the former describes his sensations as fol-
throus observer is stimulated
loows. The long \( \lambda \) end is relatively dark; from \( \lambda = 750 \) to \( \lambda = 
about 500 \), the hue is said to be one of uniform \( Y \), which, however,
varies in chroma. Between \( \lambda = 505 \) and \( \lambda = 492 \), according to
von Kries, and according to other experimenters at \( \lambda = 484 \).

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1 ROOD, C. N.: Modern Chromatics; (1875); N.Y., p. 96.
there is a narrow band which is called gray ($E \times W$). Beyond this point towards the short $\lambda$ end the hue is continuous, and is denominated B. The range between $\lambda = 430$ and $\lambda = 490$, ordinarily inducing the sensory hue violet ($R \times B$) induces a quality called B continuous with the preceding spectral regions. The point of maximum luminosity ($tw$) in the spectrum is said to lie between $\lambda = 565$ and $\lambda = 559$, a displacement from the normal of some thirty wave-lengths (normal at $\lambda = 589$). There appears to be some confusion in the exact nomenclature for the long $\lambda$ end of the spectrum among scoterythrous observers. This end is often called G instead of Y.

The Visible Spectrum as Described by a Photerythrous Observer

Since scoterythrous and photerythrous visual response show many points in common it is advisable to consider the two somewhat in parallel. The latter type is much less common than the former, and has been spoken of as "green-blindness." According to Abney the long $\lambda$ end of the physical spectrum induces a sensation quality called either R or Y. The limits of the visible spectrum are the same as for the normal sighted observer whereas in the scoterythrous observer the visible spectrum is distinctly shortened at the long $\lambda$ end. At the termination of the continuous so-called R or Y stretch the photerythrous individual finds a narrow band of gray. According to some this band corresponds with $\lambda = 518$, being nearer the long $\lambda$ end of the spectrum than the similar gray band found by

1 ROOD: loq. cit., p. 96. 2 loq. cit. 3 W.H.R.R., p. 1091
4 ABNEY, W, de W.: Colour Vision; (1895); Lond., p. 64.
5 loq. cit., p. 65.
6 ROOD: loq. cit., p. 98.
the scoterythrous, but studies made by König upon a large number of cases (twenty) of both scot- and photerythrous vision make it doubtful if there is any difference in the position of this band between the two, when the typical, rather than individual variate, forms are compared. According to König the band is situated between $\lambda = 505$ and $\lambda = 492$ in both types. Beyond this point the phtoerythrous observer reports a uniform hue called B. His point of maximum luminosity corresponds with that of the normal response, being at $\lambda = 589$.

The Comparison of Scot- and Photerythrous Visual Response. Both phot- and scoterythrous visual response fall within the so-called "dichromatic color-system." In addition to the fact, indicated by this designation, that in "color mixture" experiments the hues induced by homogeneous lights of all wave-lengths may be matched by a heterogeneous light composed of only two definite homogeneous lights in various, there are a number of other points of resemblance between the two types. Both, alike, confound lights having a normal R or G inducing power. Both, it would seem, see only three different qualities in the visible spectrum, which they usually call Y, B and gray. For both the gray band is similarly placed, and for both it can be matched by daylight and by the proper mixture of lights of $\lambda = 450$ and 700, a mixture which in the normal eye induces a bright pink. Apparently, both fail to discriminate between $L_{violet}$ and $L_b$. When their resonance curves are obtained for the fundamentals $L_p$ and $L_r$, the $L_b$ energy curves correspond but the $L_r$ curves are radically different. This difference is that which originally enabled

1 W.H.R.R., p. 1091. 2 GREENWOOD, M. Jr.: Further Advances in Physiol.; (1909); Lond., p. 397.
us to distinguish between the two types biometrically. In general, matches made by one type of dichromatic are not valid for the other. A mixture of heterogeneous lights made by a scoterythrous observer to match a certain part of the visible spectrum is generally much too luminous to suit the demands of the photerythrous observer, but it is possible to find a proportion of intensities for the two lights mixed to form the heterogeneous light which will induce a match for both photerythrous and scoterythrous observers, and when this is accomplished the lights whose sensation qualities are thus matched also induce matched sensations in the normal visual response.

The Failure of the Young-Helmholtz Hypothesis to Provide an Explanation of Dichromatic Response.....

Before we pass to the discussion of other abnormal types of visual response, let us critically consider some of the explanations of these two original types, which have been given by defendants of current visual hypotheses. On the basis of the Young-Helmholtz hypothesis scoterythrous response has long been regarded as the outcome of an absence of the resonator tuned to the long wave-lengths, while photerythrous response has been held to be due to the absence of the resonator tuned to the wave-length 505. This idea seems at present to be discredited even by the exponents of the hypothesis, themselves, It is difficult to explain the distribution of sensation quality in the spectral region of $\lambda = 590$, upon the hypothesis of an absent resonator for lights of $\lambda = 505$, and the presence of one for lights of $\lambda = 700$, or thereabouts. The Young-Helmholtz hypothesis regards sensations of Y as due to the simultaneous action of the resonators whose effect singly is the induction of R and G.
With the absence of the \( \lambda = 505 \) resonator \( M \) we should hardly expect the most intensive sensation to occur in the yellow. A similar inconsistency is involved in the case of scoterythrous vision, and in neither of these objections is it necessary to assert that the quality of the sensation actually is \( \lambda \); the simple distribution of abstract hue is inconsistent with the Young-Helmholtz assumptions with regard to the physiological primaries. From an evolutionary standpoint the scoterythrous mechanism should involve the absence of a single normally present resonator, that for \( \lambda = 700 \), while the photerythrous mechanism should require the absence of both the \( \lambda = 700 \) and \( \lambda = 505 \) resonators. But it is evident that the Young-Helmholtz hypothesis can admit of no such genetic explanation as this, for it would then be impossible that any response at all should occur—in photerythrous vision—to the long waves, to say nothing of the impossibility of the presence of two remaining and distinct hues.

The Failure of Hering's Hypothesis to Account for the Facts of Dichromatic Response

Hering's hypothesis fails entirely to account for the existence of the two distinct classes of abnormal visual response which we have described above, for he supposes a single substance to mediate both hues, \( R \) and \( G \). This substance is excited to its maximum of catabolism at \( \lambda = 700 \) (approx.) and to its maximum anabolism (cf. page 129) at \( \lambda = 495 \); these two excitabilities representing the possibility of the intensive induction of hues by lights of these wavelengths. Loss of one of these excitabilities would inevitably mean the loss of the other. But the very point which permits the sharp distinction between photerythrous and scoterythrous cases
is the fact that in one the sensation value of the long-wave-lengths remains practically the same as in the normal type. Our principal purpose in plotting the twenty case studied by von Kries (cf. Fig. 15) has been to show graphically that, from the biometric standpoint it is quite impossible to regard the two sorts of variates as members of a single germinal species; the two wholly disparate groups shown in our figure are a complete refutation of Hering's genetic explanation. Hering has endeavored to account for the existence of these two groups by postulating differences in pigmentation of the macula lutea. But there is no imaginable reason why this color should vary in such a way as to produce two independent species, such as the protanopes and the deuteranopes. Moreover, the absorption of long wave-length lights by the macular pigment is practically zero, and it is said by some investigators that the pigment is entirely absent in the fovea. Unless the pigmentation of the maculla varies in such a way that two distinct classes of retinas, with respect to the character of pigmentation, exist, in one of which five times as much "red" is absorbed as in the other, Hering's hypothesis fails to provide us with any basis for a genetic explanation of dichromatic visual response. It is impossible to suppose that both the phot- and the scotery-throus types are conditioned by the absence of the "R-G substance" alone. But it is said that Tschermak, one of Hering's disciples, has come to the decision that the above explanation of dichromatic vision cannot be defended. Ebbinghaus also emphasizes the improbability of Hering's explanation of the two types, although holding to Hering's theory in the main. The fact that Her-

1 SACHS: Arch. f. d. ges. Physiol., 1891, Bd. 50, S. 574.
2. ABNEY: loq. cit., p. 4. (over)
Hering's hypothesis fails to account for phot- and scoterythrous visual response upon the simple supposition that one of the visual substances is dropped out does not, of course, refute that hypothesis, but it never-the-less does militate against the usefulness of a viewpoint which was once highly praised on account of its supposed value as an aid in the classification of the types of color-blindness.

The Utility of Other Explanations of the Anormal Types... The failure of the Hering and Young-Helmholtz hypotheses to yield an explanation of the two forms of dichromatic vision necessitates a similar failure of the Ladd-Franklin hypothesis. Mrs. Ladd-Franklin postulates three stages of development of her hypothetical resonating molecule. The first stage enables the molecule to mediate the sensation attributes of W and B, the second those of Y and B, as well, while the final stage adds R and G. By assuming the resonators present in dichromatic vision to be in the second stage of development, no explanation is given of the two types. The situation is exactly like that faced by Hering's theory. If we imagine the third stage to be represented, but with the absence of either the R or G inducing side chains, the difficulty is similar to that which appears in the attempt to apply the Young-Helmholtz hypothesis. If we assume a mixture of stages we cannot account for the biometric distinctness of the types. The hypothesis of Wundt, being founded upon the belief that there are an indefinite number of grades of anormal visual response—with no specific types—of course fails to give an explanation of proved specificity. That of Donders, however, can be made to fit the facts and the genetic scheme.
Chapter 29: A Hint Concerning the Possible Genetic
Explanation of the Commonest Forms of Color
Blindness.

Certain Elements of the Germinal Basis of Our Hypothetical Visual Mechanism

We have postulated the existence in the retina of five specific molecular resonators, $M_w$, $M_r$, $M_y$, $M_g$, and $M_b$. Let us suppose that each of these retinal substances is the developmental outcome of a specific and distinct germinal biophores, and let us designate these biophores by the symbols: $\hat{M}_w$, $\hat{M}_r$, $\hat{M}_y$, $\hat{M}_g$, and $\hat{M}_b$, respectively. We have also, in our discussion of the evolution of the visual mechanism been led to imagine that the chromatic cortical elements, $Z_{cr}$, $Z_{cg}$, $Z_{cy}$ and $Z_{cb}$, are developmentally united into two pairs, $Z_{cr} + Z_{cg}$, and $Z_{cy} + Z_{cb}$, which are represented in the germ by the determinants $\hat{Z}_{cr}$ and $\hat{Z}_{cy}$, respectively. In Mendelian terminology, we have, then, to deal with at least seven unit characters in the discussion of the genetic relationships of the various types of visual response. Now let us imagine that in the evolution of the visual mechanism, the $\hat{M}$ and the $\hat{Z}$ characters were independently developed, that is, that one set of characters has only a functional and not a genetic connection with the other set, and, moreover, let us suppose that the members of the first set appeared in the order: (1) $\hat{M}_w$, (2) $\hat{M}_b$, (3) $\hat{M}_y$, (4) $\hat{M}_g$, and (5) $\hat{M}_r$; and those of the second set in the sequence: (1) $\hat{Z}_{cy}$, (2) $\hat{Z}_{cr}$.

The Probabilities of the Dominance of Special Combinations of Determinants

In accordance with our argument of page 420 and following, the genetic combinations of the members of the first set, in the order of the frequency of their
dominancy in present day varieties, must be: (1) \( \hat{\mu}_w \hat{\mu}_m \hat{\mu}_y \hat{\mu}_g \hat{\mu}_r \), (2) \( \hat{\mu}_w \hat{\mu}_b \hat{\mu}_y \hat{\mu}_g \), (3) \( \hat{\mu}_w \hat{\mu}_b \hat{\mu}_y \), (4) \( \hat{\mu}_w \hat{\mu}_b \), and (5) \( \hat{\mu}_w \). And, similarly, of the second set: (1) \( \hat{\mu}_y \hat{\mu}_b \hat{\mu}_c \), (2) \( \hat{\mu}_y \hat{\mu}_b \). In either series the most improbable event of all is the absence of every member.

We have given reason—on page 441—for the supposition that \( \hat{\mu}_r \) is a relatively late acquisition of the germ plasm, and that, possibly, it takes the place in the normal mechanism of some previous determinant—and resonator—\( \hat{\mu}_r \)—and \( \hat{\mu}_r \). If this is the case we should expect that in the greater proportion of the abnormal visual types discoverable by the biometric methods outlined in Chapter 23—and types possessing hereditary rather than pathological determination—the element \( \hat{\mu}_r \) will be absent from the germ plasm. In a smaller proportion of the variates \( \hat{\mu}_r \) will also be absent, and so on, — in the first set. Since the second set of determinants has nothing to do with the first, there will be certain cases in which \( \hat{\mu}_c \) is absent, but \( \hat{\mu}_r \) present, but there will be more in which both of these factors are missing. In other cases, both \( \hat{\mu} \) factors may be gone, without the lack of any of the members of the first series. In addition to the normal type and the totally blind there are obviously ten possible combinations of the abbreviated germinal structures made possible by the above scheme. The most probable of these is \( \hat{\mu}_w \hat{\mu}_b \hat{\mu}_y \hat{\mu}_g \hat{\mu}_c + \hat{\mu}_y \hat{\mu}_b \). It would seem, however, that the combinations: \( \hat{\mu}_w \hat{\mu}_b \hat{\mu}_y \hat{\mu}_c \hat{\mu}_r + \hat{\mu}_y \hat{\mu}_b \hat{\mu}_c \) and \( \hat{\mu}_w \hat{\mu}_b \hat{\mu}_y \hat{\mu}_c + \hat{\mu}_y \hat{\mu}_b \hat{\mu}_c \). In order to avoid the conclusion that such in the case we must admit that the \( \hat{\mu} \) and \( \hat{\mu} \) sets of determinants are not entirely without interrelationship, and that a combination of two ancient germinal architectures is more likely than a combination of one ancient and one modern.
The Germinal Formulae of... Several Hereditary Forms... Of Anormal Visual Response

Upon the foundation provided by the above genetic analysis we may erect the framework of an explanation of several of the existing anormal types of visual response. The analysis in question gives us some basis for affirming that the order of probability of certain anormal germinal formulae is as follows: (1) \( \overset{\circ}{w}w_{D}b_{D}r_{Y}g_{Y} + \overset{\circ}{z}_{cyb} \), (2) \( \overset{\circ}{w}w_{D}b_{D}r_{Y}g_{Y} + \overset{\circ}{z}_{cyb} \), (3) \( \overset{\circ}{w}w_{D}b_{D}r_{Y}g_{Y} + \overset{\circ}{z}_{cyb} \overset{\circ}{z}_{org} \), etc. Now we will suppose formula (1) to be that of the protanopic or scoterythrous type, discussed above (Chap. 28), formula (2) to be that of the deuteranopic or photerythrous type and formula (3) to be that of the so-called anomalous trichromatics. Other germinal formulae may readily be written and their relative probabilities suggested. We must admit the existence of a tendency for coeval combinations in the two series to appear in conjunction, so that the formula: \( \overset{\circ}{w}_{w} + \overset{\circ}{z}_{cw} \) may not be so improbable as at first it might seem. \( \overset{\circ}{z}_{cw} \) is employed to designate the germinal determinant of the cortical luminosity element which will, of course, be present, even in the entire absence of \( \overset{\circ}{z}_{org} \) and \( \overset{\circ}{z}_{cyb} \). This last formula we shall consider the most probable one for the totally color blind.

The Explanation of Scoterythrous Visual Response... Dr. Joy Jeffries found 1 that out of 10,397 variates examined by him in Boston and vicinity, 286 were scoterythrous, 75 photerythrous, and 68 partially color-blind. In harmony with our above discussion we suppose formula (1) to be that of the scoterythrous cases. Let us see how this formula gives

1 JEFFRIES, J.: Color-blindness; Its Dangers and Detection; (1879); Boston; p. 75.
with the facts deduced in the empirical study of this type of visual response, the facts which we have discussed in the preceding chapter in connection with other hypotheses. Our germinal formula calls for the absence of the resonator $M_r$ and for that of the $R$- and $G$-cortical-chromatic elements. With the lack of the latter the observer would, of course, be unable to discriminate between different wave-lengths by means of the reactions of the $M_r$ and $M_g$ resonators; hence he would confuse "red" and "green." But $M_r$ is absent, and for this reason his visible spectrum will be truncated at the long $\lambda$ end. For the same reason, the point of maximum luminosity in the spectrum will be shifted towards the short $\lambda$ end, since the rise to the maximum will be determined by the $M_y$ and $M_g$ resonators only (cf. Fig. 9). A glance at our diagram of the resonance functions (page 330) will show that between $\lambda = 700$ and $\lambda = 500$, the spectrum of the scoterythrous observer should possess the hue $Y$, only, while between $\lambda = 500$ and $\lambda = 390$, it should exhibit the hue $E$, alone, the places of maximum saturation in each region being approximately central in position. At $\lambda = 500$, where the $M_y$ and $M_b$ curve intersect, there should be a gray ($W \times B$) band of greater or less width, owing to the dominance of the complementation ions in this region. It will be noticed that these deductions from our theory are in complete accordance with the facts which were stated in the preceding chapter. 28.

The Explanation of Photerythrous Visual Response.....

Our formula for the photerythrous type of visual response demands the absence of the $R$- and $G$-cortical-chromatic elements only, all of the retinal resonators being present. It
follows that the limits of the visible spectrum for observers belonging to this species will be the same as those for the normal observer, that the position of maximal luminosity will also be the same. It also follows that the only hues appearing in the spectrum will be Y and B and that these will be distributed in the same fashion as in the visible spectrum of the scoterythrous observer, and that the position of the neutral band will be the same as for the latter. Moreover, it is easy to see that in comparing these two types in the manner fully described on page 412 ff. an illustrated in Fig. 15 the scoterythrous subject will require a much greater intensity of $L_{\text{red}}$ for a specific match than will the photerythrous, on account of his lack of the $M_r$ resonator. "Red" for the scoterythrous is pure physiological "yellow", and a glance at von Kries' curves shows that for the scoterythrous subject this excitation exhibits a maximum at $\lambda = 571$. This, it will be noted, is the position of the $M_y$ maximum in our diagram (page 330). Similar curves for photerythrous observers possess a maximum at $\lambda = 603$, the outcome of a compromise between the luminosity effect of $M_r$ and the luminosity-hue effect of $M_y$. It is clear that a superficial analysis, at least, offers no evidence which can be employed to refute the formula which we have suggested for photerythrous visual response.

The Anomalous Trichromatics and Total Color Blind......

Concerning the anomalous trichromates time forbids that we should present an exhaustive analysis. The work of von Kries and others has clearly shown that these individuals form a distinct species. The investigations carried out by Donders, however indicate that the problem involved is a complex one, and

1 Cf. HELMHOLTZ: Handbuch.; (1911); Bd. 2, S. 337, Fig. 76.
it is likely that our formula may require modification. It is unnecessary to give special attention to the explanation of total color blindness upon a genetic basis. In the majority of cases the formula appears to be that indicated, no hues being experienced, and the maximum brightness being that natural to the \( M_w \) resonator. One case, reported by Magnus, however possessed a maximum at \( \lambda = 580 \), that of normal response. The formula of this variant was undoubtedly: \( \frac{a}{n} \frac{a}{b} \frac{g}{m} \frac{r}{g} + \frac{a}{c} \). Total color-blindness is usually accompanied by photophobia, indicating the exclusive functioning of the \( M_w \) resonator, which is inoperative in daylight.

The Possibilities of our Genetic Scheme... The above explanations are presented merely as illustrations of the manner in which the elements of our hypothesis may be applied in the explanation of the various types of visual response. It is clear that besides the ten types which we have asserted may be expected to occur in the course of combination of the members of the two genetic series of germinal structures, other germinal formulae may be written which cannot be developed from the genetic series, but which are possible. For example, any single resonator may be dropped out while the others remain. Twenty-seven distinct combinations may be written by the use of the five resonator determinants alone. Formulae which do not fall into the genetic series must, of course, be adjudged the outcome of pathological, rather than hereditary processes. In the discussion of cases in which single resonators have been dropped, without an accompanying lack of cortical machinery, it will be necessary to make use of the conceptions which we have developed on page 117 ff. with regard to the meanings of the sensation-des-
criptive terms employed by the experimenter and the observer, since in the absence of $M_r$—for example—every sensation would be tinged with G, owing to the entire absence of the complementation reaction for $I_g^+$ ions.

"Yellow-blue" Blindness.... A single example of the pathological types of visual response may be briefly considered. Hering has laid great stress upon the existence of a species of visual response in which the sensation quality is restricted to the hues R and G; he supposes this condition to be due to the absence of the $M_{by}$ substance postulated in his theory. Several cases of this sort have been studied, but they are of rare occurrence and—except in a single instance—have been accompanied by recognizable pathological cerebral conditions. Upon our hypotheses visual response of this character must obviously be due to the disease of the cortical elements $Z_{cy}$ and $Z_{ob}$ or to the absence of the corresponding resonators. The position of the neutral band in the visible spectrum of the yellow-blue blind observer is between $\lambda = 596$ and $\lambda = 568$. It will be noticed that this is the location of the point of intersection of the $M_r$ and $M_g$ curves in our Fig. 9. The most saturated green is seen at $\lambda = 532$. This again is in harmony with the maximum of $m_g$ as we have represented it.

1 W. H.R.K., p. 1093 fL
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Chapter 30: The Explanation of the Results of the Campimetry of the Hues.

Hypothesis of the Field Distribution of the Specific Components of Visual Response

To explain the facts which have been adduced by students of the manner in which sensory quality is related with the position of the sensation in the visual field (cf. page 108), we may make the following assumptions—postulates—based upon evolutionary considerations. In the development of a new factor in the visual mechanism there would naturally be a tendency for development to commence in that portion of the visual structure which was functionally most important, most favorably situated. This portion being the center of the retina and its connections, it follows that when the chromatic resonators were organized within the retinal end organs, and the cones were produced, this development started in the axis of the retina and spread centrifugally. As an outcome of the superior efficiency of the chromatic mechanism all of the achromatic elements—the cones, and $M_w$—were finally driven out of the retinal center and the rodless fovea was formed. Similarly the resonators $M_r$ and $M_g$ must first have appeared in the medial region, from which region they invaded the more peripheral parts. Since the resonators $M_y$ and $M_b$ were more forehand, however, these latter elements must have spread farther in the field. If we express this same development in terms of cerebral evolution—supposing the resonators to have been originally well distributed—$Z_{or}$ and $Z_{cg}$ must be considered more rare in connection with peripheral retinal cones than in connection with more central cones, on account of the original appearance of the chromatic cortical elements.
in conjunction with the most functional parts of the visual syner-
gic mechanism. Only here would they be surely utilized and pre-
served. Since $Z_{cy}$ and $Z_{cb}$ appeared first, however, these will
have a broader distribution in the cortex than $Z_{cr}$ and $Z_{cg}$.
If we explain the results of the campimetry of the hues in terms
of cortical elements, we must say that the complete cortical
elements corresponding with the cones of the fovea are provided
with $Z_{cy}$, $Z_{cb}$, $Z_{cr}$ and $Z_{cg}$, all of the cortical receivers con-
ected with the foveal cones have chromatic elements of the four
specified varieties. As we pass centrifugally in the retina, how-
ever, the corresponding cortical receivers begin to lose their
chromatic elements and in such a way that the $Z_{cr}$ and $Z_{cg}$ elements
fall off more rapidly than do $Z_{cy}$ and $Z_{cb}$. We do not conceive
that in any portion of the synergetic mechanism, however remote from
foveal connections, there are absolutely no representatives of
the chromatic cerebroidea; the chromatic elements merely become
sparser among the peripheral structural units. This dilution of
the chromatic constituents of the mechanism towards the peripheral-
ly connected parts must undoubtedly be referred to germinal caus-
es, and since we have found reason for supposing that $Z_{cy}$ and $Z_{cb}$
are governed by a single determinant, $Z_{cyb}$, and $Z_{cr}$ and $Z_{cg}$ by
another single determinant, $Z_{crb}$, it follows that the complemen-
tary elements will everywhere be accurately balanced against each
other. Whether or not there is a parallel diminution in the
prevalence of the several molecular resonators in the retinal
units may be left undecided. Certain results obtained by von
Kries, showing that the luminosity values of the spectral colors
do not change with change of the position in the field at which
they appear, seem to indicate that the chemistry of the retinal cones is a fixed quantity, irrespective of situation. If this is true it is a rather remarkable fact, for the relative non-functionality of the chromatic resonators in the peripheral cones might be expected to bring about—or be reflected in—a certain vestigial or rudimentary condition of these cones with respect to the characters in question. 1

The Simple Hues as Revealed by Hue Campimetry......... Hess finds 2 that there are three homogeneous lights which, if employed in the stimulation of different parts of the retina induce a constant sensory hue, although their chroma, of course, varies with nearness to the fovea. These lights have wave-lengths of $\lambda = 574.5$, $\lambda = 495$, and $\lambda = 471$, inducing Y, G, and B respectively. It will be seen that the first two values represent the points of intersection of the $M_r$ and $M_g$, and the $M_y$ and $M_b$ resonance function curves of our diagram (Fig. 9). At these points one pair of complementary ions is completely removed from the response, so that any alterations which may occur in the capacity of the cortex to discriminate differences in the concentrations of these ions, resulting from the movement of the constant stimulus over the retinal field, will be without effect upon the sensory hue. The value $\lambda = 471$, again, represents the second intersection of the $M_r$ and $M_g$ curves. In order to induce a red which does not suffer change in hue with movement over the visual field (constant stimulus) it is necessary to mix a certain amount of $L_{471}$ with $L_{760}$. The reason for this is evident from our figure, for—as we have continually insisted—there is a powerful $m_y$ excitation underlying the sensory hue of

(over)

spectral red; in order to neutralize the effect of this excitation a certain $\mathbf{m}_b$ must be added.

Changes in Sensory Hue Induced by Movement of a Constant Stimulus from Fovea to Periphery. If a stimulus which effectively excites more than one of the chromatic molecular resonators be moved from the fovea towards the ora serrata the corresponding sensation will undergo an alteration in sensory hue, owing to the disappearance of the $c_r$ and $c_g$ cortical responses, -- provided, of course, that the light employed is relatively homogeneous. A glance at our figure (page 330) will enable us to prophesy the exact change that will take place. If the central hue is approximately G, the peripheral one may be either B or Y, according as the--homogeneous--light employed falls on one side or the other of the $M_y M_b$ intersection at $\lambda = 495$. If the first hue is R, it must become Y at the periphery; a violet will turn to blue, while a Y may be modified into either an R or a G. All of these prohesses are fulfilled. 1

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LIST OF THE MOST IMPORTANT SYMBOLS USED IN THIS THESIS.

Note: The symbols are arranged in alphabetical order, capitals preceding lower case letters. The Greek letters follow their phonetic equivalents in English. Where alphabetical criteria could not be applied the simpler terms have been given precedence.

As stated on pages 78-79 we have employed lower case letters for a quantitative meaning, and upper case letters for qualitative meanings.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>$AB_s$</td>
<td>The aesthesogen which with $C_s$ forms the basis for the chemical synthesis of any resonator $M_s$. (p. 220.)</td>
</tr>
<tr>
<td>$a$</td>
<td>The cross-section (area) of any specified fascicle of light rays. (p. 282).</td>
</tr>
<tr>
<td>$ab_s$</td>
<td>The concentration of the aesthesogen $AB_s$ in any retinal element: molecules per retinal element. (p. 269)</td>
</tr>
<tr>
<td>$B$</td>
<td>The hue: blue. One of the possible attributes of the elementary visual sensation, $S$. (p. 92)</td>
</tr>
<tr>
<td>$b$</td>
<td>The blueness of any elementary visual sensation, measured in difference limina from zero blueness. (p. 92)</td>
</tr>
<tr>
<td>$B$</td>
<td>The factor of tint: black. An attribute of the elementary visual sensation, $S$. (p. 94)</td>
</tr>
<tr>
<td>$b$</td>
<td>The blackness of any elementary visual sensation. Measured in difference limina from zero blackness.</td>
</tr>
<tr>
<td>$b_m$</td>
<td>The greatest possible blackness of any sensation.</td>
</tr>
<tr>
<td>$C$</td>
<td>The elementary visual cerebrosis. (p. 61) (p. 252)</td>
</tr>
<tr>
<td>$C_s$</td>
<td>The $s$ component of any elementary visual cerebrosis, as $C_r$, $C_y$, $C_g$, $C_b$, $C_w$, etc. (p. 253)</td>
</tr>
<tr>
<td>$c$</td>
<td>The intensity of the visual cerebrosis, $C$. Molecules (ions) per cortical element. p. 250</td>
</tr>
<tr>
<td>$c_s$</td>
<td>The intensity of the component $s$ of any elementary visual cerebrosis, as $c_r$, $c_y$, etc. (p. 253)</td>
</tr>
<tr>
<td>$c_s'$</td>
<td>The initial cerebral intensity of the $s$ component of the visual cerebrosis. Number of ions per elementary cortical receiver. (p. 263)</td>
</tr>
</tbody>
</table>
$c^+$
Total initial cerebral intensity. Sum of all of the positive ions per elementary cortical receiver. (p. 360.)

$\bar{C}_s$
One of the aesthesogens of the molecular resonator, $M_s$. See: $\bar{A}_s$. (p. 220)

$\bar{c}_s$
Concentration of the above aesthesogen. (p. 220)

$d$
Distance of any $S$ from the fixation point in the visual field. (p. 85)

$\Delta H$
The qualitative difference between two $S$'s in point of sensory hue. (p. 90)

$\Delta$S
The whole qualitative difference between any two $S$'s, the sensation differential of p. 89.

$\Delta$
Prefix for any visual limen, as $\Delta c$. (p. 284)

$\Delta c$
Cortical discrimination limen. (p. 284)

$\Delta c_s$
Cortical discrimination limen for any component $c_s$ of the visual cerebrosum. (p. 284 f)

$\Delta m_s$
The stimulation limen of the component $s$ of the elementary visual response. Change in $m_s$ required to bring about the cortical change $\Delta c_s$. (p. 284)

$\Delta(tae)$
Energy threshold. (p. 295)

$\delta$
Prefix for any quantitative difference. (p. 92)

$E$
The experimenter in the psychological experiment. (p. 116)

$\eta$
Impulse loss: ions lost per second per unit length of the elementary visual conductor. (p. 247)

$\eta_s$
Impulse loss of the $s$ component of the impulse, as $\gamma_r$, $\gamma_g$, $\gamma_y$, etc. (p. 266)

$\xi\eta$
Total impulse loss: ions lost from the elementary visual conductor by any element of impulses passing from the retinal element to the cortex. (p. 247)

$f$
Force confining the visual impulse, so that: $\eta = k(\frac{f}{\xi})$ (p. 248)

$f^o(\ )$
Function: $i_+ = f^o(m)$. Stimulation function. (p. 285)

$f_{\alpha}(\ )$
Resonance function for the molecular resonator $M_s$. $m_s = f_{\alpha}(\lambda)$. Sometimes written: $f_n(\ )$. (p. 2857)

$G$
The hue: green. A possible attribute of the elementary visual sensation, $S$. (p. 93)
The greenness of any elementary sensation, S. Measured in differente limina from zero greenness. (p. 92)

H

The sensory hue of any sensation, S. Total chromatic quality.

H_a

The complementary sensory hue to H. (p. 93)

H_c

The complementary sensory hue to H_a.

h

The chroma of any elementary visual sensation, S. This is the equivalent of "degree of saturation." (p. 94).

h_a & h_c

Quantitative measures of the complementary hues H_a and H_c. (p. 93)

I

The elementary visual impulse. (p. 61)

I

A visual image. (p. 110)

I_s+

The positive ion liberated in the dissociation of the molecular resonator M_e. E.g.: I_r+, I_w+, etc. (p. 259)

I_s-

The negative ion do.

I_w+

The native positive ion of the cortical luminosity element. (p. 260)

I_w-

The native negative ion, do.

I_w'+

The complementation ion. Equivalent to \( 2 I_w' + \). (p. 273)

I

Visual impulse intensity. Ions passing through any cross-section of the elementary visual conductor, per second. (p. 246)

I_a & I_k

Complementary components of the impulse intensity. (p. 272)

I_s

Component of the impulse intensity due to the resonator M_e, as \( I_r, I_y, \) etc. The complementation reaction also contributed a component. (p. 250 and p. 266)

I_r

Impulse intensity at the retinal element.

I_r

Component impulse intensity at the retina. (p. 335)

j_h'

The specific brightness of the hue, H'. (p. 361)

k

Any constant.
\( k_i \) Constant in \( \mathbf{2} \gamma = k_i \gamma_{av} \). (p. 247)

\( k'_i \) Constant in \( \mathbf{2} \gamma = k'_i \gamma_c \) (p. 248)

\( k''_i \) Constant in \( \mathbf{2} \gamma = k''_i \gamma_r \) (p. 313)

\( k_n \) Constant in \( \rho = k_n \rho \) (p. 316)

\( k_{sw} \) etc. See pages 360 ff.

\( L \) Light, as stimulus.

\( L_\lambda \) Light of wave-length \( \lambda \). Homogeneous. (p. 151)

\( \lambda \) Wave-length of light in \( 10^{-7} \) cms. \( \lambda = c/n \), where \( c \) is the velocity of light in free space. (p. 151)

\( M_r \) etc. Molecular resonator for \( R \), etc. The chromatic resonators are described on p. 267, the achromatic do.

\( M_{crg} \) Complementation molecule for ions \( I_{r+} \) and \( I_{g+} \). (p. 270)

\( M_{cyb} \) Do. for \( I_{y+} \) and \( I_{b+} \).

\( m_s \) Concentration of the molecular resonator \( M_s \). Molecules per retinal element. (p. 212).

\( \dot{m}_s \) Rate of dissociation, or reaction velocity of \( M_s \). (p. 212)

\( n \) Frequency of light \( L \). Sometimes used as a general subscript, in place of \( s \). (p. 151)

\( O \) The observer in the psychological experiment. (p. 116)

\( O \) Zero.

\( P \) The elementary visual stimulus. (p. 60)

\( \gamma_S \) Cortical dissipation for component of visual response, \( s \). (p. 250, 254)

\( q_S \) Light sensitivity of the resonator \( M_s \). (p. 213) (p. 268)

\( R \) The hue: red. A possible attribute of the elementary visual sensation, \( S \). (p. 92)

\( r \) The redness of the sensation \( S \). Measured in difference limina from zero redness. (p. 92)

\( \rho_s \) Resonance gradient of the resonator \( M_s \). (p. 214) (p. 268)
The elementary visual sensation. (p. 59)

Generalized subscript. Once used as general quantitative description of S.

Impulse density. (p. 246)

Qualitative term for the tint of S. (p. 93)

Quantitative measure of T. (p. 93)

Luminosity of S. Equivalent to "brightness", "intensity," "Helligkeit", etc. (p. 95)

The time. (p. 282)

Impulse velocity. (P. 246) (p. 288)

The elementary visual response. (p. 58) See pp. 62-63.

The component of tint, white. A constant attribute of the elementary visual sensation, S. (p. 94)

The degree of whiteness of S. (p. 94)

The elementary visual stimulation process. (p. 60)

The hue: yellow. A possible attribute of the elementary visual sensation, S. (p. 92)

The yellowness of S. (p. 92)

Any visual structure (elementary). (p. 57)

Cortical chromatic elements. (p. 261)

Cortical discrimination element. (p. 283)

Cortical luminosity element. (p. 260)

Cortical receiver. (p. 259)

Retinal element of structure. (p. 289)

Any stimulated portion of the retina. (p. 376)

Any simultaneously (see above) unstimulated portion of the retina. (p. 376)

Rate of dissipation of negative ions in the retina from any retinal element. (p. 316)

The sign o over any symbol for a structural element indicates the germinal determinant of that element.
ADDENDA.

$t_c$  Impulse intensity at the cortical element.
$k_c$  Constant in $\psi = k_c c$.
$k_r$  Constant in $\zeta_r = k_r i_+$.
$e$  Light intensity.
$f_{es}(\ )$  Stimulation function: $\zeta_r = f_{es}(e)$. (p. 321)
$f_{es\lambda}(\ )$  Complete stimulation function: $\zeta_r = f_{es\lambda}(e, \lambda)$.
(p. 326)

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