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COLOR-VISION.*

THE domain of physiological optics, formerly much frequented by students of physics, has of late been administered chiefly by psychologists. So far is this true that I have hesitated in preparing an address upon a subject in this realm, lest I should be accused of passing entirely beyond that borderland which lies between us and our sister science, of trespassing in a foreign country, and risking international complications. Yet a subject which has owed its development to Newton and Young, Maxwell and Helmholtz, to mention no other names, can hardly be out of place here. The methods of investigation are largely those of the physicist, the phenomena attend every optical research, the results are of frequent physical application. Within the past few years, however, most of the work on color-vision has been done by other hands, and the results have not appeared in the physical journals. It seemed worth while, therefore, to review briefly the progress of scientific theory in this direction, and to sum up, so far as possible, the present state of our knowledge.

For our purpose we must go back as far as Sir Isaac Newton, to whom we owe the first definite and intelligible hypothesis as to the nature of color-vision.

*Address of the Vice-President before Section B— Physics—of the American Association for the Advancement of Science, August, 1898. "If at any time," he says, "I speak of Light and Rays as coloured or endued with Colours, I would be understood to speak not philosophically and properly, but grossly, and according to such Conceptions as vulgar People in seeing all these Experiments would be apt to frame. For the Rays to speak properly are not coloured. In them is nothing else than a certain Power and Disposition to stir up a Sensation of this or that Colour."

"For as Sound in a Bell or musical String or other sounding Body is nothing but a trembling motion, and in the Air nothing but that Motion propagated from the Object, and in the Sensorium 'tis a Sense of that Motion under the form of Sound; so Colours in the Object are nothing but a disposition to reflect this or that sort of Rays more copiously than the rest; in the Rays they are nothing but their dispositions to propagate this or that motion into the Sensorium, and in the Sensorium they are Sensations of those Motions under the forms of colours."*

Again, with greater definiteness, Newton writes: "To explain colours, I suppose that as bodies of various sizes, densities, or sensations, do by percussion or other action excite sounds of various tones, and consequently vibrations in the air of different bigness, so the rays of light, by impinging on the stiff refracting superficies, excite vibrations in the ether * * * of various bigness; the biggest, strongest, or most potent rays, the largest vibrations; and others shorter, according to their bigness, strength, or power; and therefore the ends of the capillamenta of the optic nerve, which pave or face the retina, being such refracting superficies, when the rays impinge upon them, they must there excite these vibrations, which vibrations (like those of sound in a trunk or trumpet) will run along the aqueous pores or crystalline pith of the capil-

*Opticks : 3d edition, 1721, p. 108.

lamenta, through the optic nerve into the sensorium; and there, I suppose, affect the sense with various colours, according to their bigness and mixture; the biggest with the strongest colours, reds and yellows, the least with the weakest, blues and violets; the middle with green; and a confusion of all with white, much after the manner that in the sense of hearing, Nature makes use of the aërial vibrations of several bignesses, to generate sounds of divers tones; for the analogy of Nature is to be observed."*

These passages are quoted—and several others might be added—to show that Newton ascribes no peculiar function or activity to the terminals of the optic nerve. They are set in vibration by the rays of light; their vibrations are transmitted to the higher regions of the sensorium, where they become sensations of light and color. As to the physical nature of the rays themselves, or the reason why they should excite in the nerve-fibres vibrations of different length, Newton makes no guess.

This is a definite theory of color-perception, and, as Rutherford has pointed out, one of great value, but presenting obvious difficulties.

Some of these difficulties led Thomas Young to that modified form of Newton's views, which in the famous Bakerian lecture, he describes as follows: "Since * * * , it is probable that the motion of the retina is rather of a vibratory than an undulatory nature, the frequency of the vibrations must be dependent on the constitution of this substance. Now, as it is almost impossible to conceive each sensitive point of the retina to contain an infinite number of particles, each capable of vibrating in perfect unison with every possible undulation, it becomes necessary to suppose the number limited, for instance, to the three principal colours, red, yellow and blue * * * and that each of the particles is capable of being put

*Quoted by Young, Phil. Trans., 1802, p. 19.

in motion less or more forcibly, by undulations differing less or more from a perfect unison; * * * and each sensitive filament of the nerve may consist of three portions, one for each principal colour." Young, as is well known, afterward substituted green for yellow, in his triad of principal colors.

It is to be observed that the 'particles' spoken of in the above quotation, as vibrating in unison with the undulations of light, are not to be considered as molecules, in the modern sense. He speaks of them as particles, then as sensitive filaments, and in a later paper on the same subject as 'sympathetic fibres.' A supposition, such as has been urged, that Young is here speaking of molecular constitution, and anticipating the photo-chemical theories of our own day, is an anachronism. Young is thinking of the wave-theory of light, and of sympathetic vibrations, or, as we should say, of resonance. One who meant chemical decomposition would not speak of the shattered molecules as sympathetic fibres. Young, in fact, is not consciously proposing a new theory, much less one so startlingly different. He is simplifying Newton's, making for that purpose four hypotheses, three of which, as he remarks himself, 'are literally parts of the more complicated Newtonian system.' Young's theory seems to have attracted little attention, until brought once more to public notice by Helmholtz, in 1860.

Helmholtz suggests one objection to the theory, and a modification to obviate the objection, but remarks that the essence of the theory does not lie in this or that special assumption, but in the fact that the color-sensations are conceived as compounded out of three entirely independent properties in the nerve-substance.

Therefore, he says, if only for the sake of clearness of representation, he uses Young's original and simple form of statement, ascribing the different color-sensa-

tions to three-kinds of nerve endings in the retina, sensitive respectively to red, green and violet light, the sensation of white to the equal excitation of all three sets of nerve-fibres, and color-blindness to the absence of one or more of the sets of such fibres. He puts into Young's words, however, an entirely different meaning, by classifying Young's hypothesis as 'only a special application of the law of specific senseactivities.' This statement, a most natural one to a pupil of Johann Müller, changes the whole character of the theory, and makes it really a new one.

The hypothesis in this simple form met very well the conditions of normal vision. and the cases of color-blindness thus far studied. Difficulties soon arose. Colorblindness, especially red-blind persons, persisted in calling the principal colors seen in the spectrum, yellow and blue, instead of green and blue, as they should have done if the red sensation were simply absent. It was long supposed that this was merely a question of naming the colors, and that those actually seen were green and blue. So lately as 1892 the report of the British Association committee on color-vision contains colored spectrum-plates, in which the spectrum as seen by a red-blind person is shown as composed of green and blue, while that seen by a green-blind person is formed of red and blue. Abney prefixes the same plate to his Tyndall lectures on color-vision, published in 1894. But in 1881 Hippel* and Holmgren† had examined the vision of a person, one of whose eyes was normal, the other typically color-blind. All the long-waved end of the spectrum was described as yellow, the sensation being tested by comparison with the normal eve. Other cases of color-blindness, arising from disease, corroborate this testimony.

*Arch. f. Ophthal., XXVI. (2), p. 176, 1880; XXVII. (3), p. 47, 1881.

† See Proc. Roy. Soc., No. 209.

It is evident that a simple absence of one of the fundamental sensations is not enough to account for the facts.

But more than the ordinary color-blindness comes into the question. It was discovered that the normal eye is color-blind by indirect vision, the condition gradually increasing from the central portion outward, and culminating in the periphery of the retina in absolute insensibility to color. The sensation of white cannot in this case be produced by a mixture of three colorsensations, because color-sensation does not exist.

In 1777 was described, in the Philosophical Transactions of the Royal Society, the well-known case of the shoemaker Harris, apparently the first recorded case of complete color-blindness. In 1871 Donders made a careful study of another case. So rare is this defect, however, that so assiduous an observer as Holmgren in 1877 had never seen it and doubted its existence, and in 1889 Helmholtz simply passes it by, saying that the eye so affected is always in other ways ailing and sickly, the implication being that the effect was so far from the ordinary and so pathological in character that it need not be considered. But by 1892 a sufficient number of such cases had been examined to establish the existence of this as a distinct type of color-vision, and one which must be accounted for.

A third and even more striking departure from the simple conditions of the original theory was found in the remarkable change in the character of color-sensations in faint light, the spectrum becoming simply a colorless strip of graduated brightness.

We have then three different types of varying color sensibility :

1. In the eyes of different persons, beginning with the normal-eyed, passing through the variation studied by Rayleigh and Donders, which while recognizing all colors, yet in the character of the sensations makes a step toward green-blindness, then the two well-marked divisions of the colorblind, red- and green-blind, and finally the eye which perceives no color. These different classes are well marked, and few intermediate forms are found.

2. In the same eve, under differing degrees of brightness. As the spectrum gradually diminishes in brightness the colors change. Red tends toward yellow, yellow toward green, green becomes bluish. All the colors vanish by degrees, red disappearing first, and the spectrum, still visible through the greater part of its length, appears without color. Here the intermediate stage is a sort of red-blindness, but the final result is the same for all eyes, that is, the distribution of brightness for the normal and the color-blind eye appears to be precisely the same, a circumstance, as we shall see, of much importance.

3. In a single eye, passing from the center outward. The fovea and the zone surrounding it are sensitive to all colors. Outside of this the eye becomes gradually insensitive to color, the sensation of red and green disappearing first, afterwards yellow, and finally blue. The outer part of the retina is insensitive to all color, but its condition may be quite different from that of the eye of a totally color-blind person, or a normal eye in faint light.*

In attempting to account for these varied phenomena the Helmholtz theory loses its striking simplicity. It is no longer possible to explain color-blindness by the absence of one or more sets of sensitive fibres, or the white seen by a totally color-blind retina, as compounded from the three fundamental sensations, in any ordinary way.

Helmholtz, in 1860, made the suggestion, which was afterward amplified by Fick and König, of a possible changeability in the

*von Kries, Centralblatt f. Physiologie, X., pp. 745-749, 1896.

character of the three fundamental sensations. Albert, in 1882, from a study of the color changes in faint light, pointed out the direction and character of the corresponding sensation-changes.*

A method by which such changes might be brought about was not difficult to suggest. The idea of Newton and Young, of nerve-fibres vibrating in unison with the light-waves, had grown increasingly improbable as, on the one hand, the rate of vibration of light became known, and on the other the maximum rapidity of vibration transmissible by a nerve-fibre, which is a quantity of an entirely different order. Hence most modern theorists have turned to photo-chemical action, and Helmholtz among the rest, although with characteristic caution, he advocates no particular form of light effect, resting the claims of his theory, in the second edition of his great book as in the first, on the physical possibilities of representing all colors by means of three. But if we suppose red-sensitive, green-sensitive and violetsensitive molecules, there is no difficulty, when one thinks of modern photographic processes, in supposing that the green-sensitive substance, for example, may be so chemically changed as to coincide in character with the red-sensitive. Each would send to the brain the impression of its own characteristic color, while each would be affected in exactly the same manner by any given light. In other words, the color curve corresponding to the sensation of the fundamental green in the Young-Helmholtz theory would be more or less perfectly superposed upon that of the fundamental red.

As a result, there would be no more sensation of green or red, but only of their compound, yellow. Now this is just what a color-blind person sees, as Hippel and Holmgren showed in their long-neglected papers already referred to.

* Albert, Wied. Ann., 16, p. 129, 1882.

So peripheral color-blindness may be explained by a gradual approximation of the three color-substances, and a gradual superposition of the corresponding sensationcurves, until in the outer zone all three coincide.

But when we attempt to apply this suggestion to all the changes noted before, in ordinary color-blindness, peripheral colorblindness and twilight color-blindness, as von Kries happily calls it, the shifting of the curves becomes so great and so various that we realize that we are dealing no longer with a scientific theory, but with fanciful and arbitrary arrangement. As a first approximation, the Young-Helmholtz hypothesis is valuable, leading to simple and definite connections between great numbers of facts. As a detailed explanation of existing phenomena it is unsatisfactory, and growing more so daily.

One thing is becoming steadily evident, that the sensation of brightness, perhaps also the sensation of white, must be accounted for in some other way than as a summation-effect of separate color-sensations. Another class of phenomena points yet more directly to this view. I refer to the discovery of Rood that the effect of sudden variations in brightness, the 'flicker' sensation, is dependent on brightness alone, and not upon color. It is difficult for one who has seen how easily and definitely a red and a gray, or a red and a blue, can be compared in brightness by this method, to believe that brightness is not an independent sensation. The words of Helmholtz are worth quoting here. "As to myself," he says, "I have always the feeling that in photometric comparison of different colors it is a question, not of the comparison of one sort of magnitude, but of the combined effects of two, brightness and color, of which I cannot form a simple summation and of which I can give no scientific definition."

The strongest point of attack upon the

Young-Helmholtz color-theory has, in fact, always been the explanation of the whitesensation, and one of the principal advantages of the theory proposed by Hering in 1874 was the separation of the whitesensation, which he identified with the sensation of brightness, from special connection with the color-sensations, or rather his including it, upon the same level, in the list of his three sets of opposing colors, blackwhite, red-green, yellow-blue.

A photo-chemical substance is supposed to exist in the eye-where it is not decided -which possesses the remarkable property that if acted upon by light of one wavelength its molecules are dissociated or dissimilated; if acted upon by light of another wave-length they are built up or assimilated again. This substance exists in three forms : One is, let us say, dissimilated by red light, assimilated by green ; one is similarly acted upon by yellow and blue, and one by white and black. There are thus six color-processes, arranged in three pairs. They are antagonistic in character, so that if red and green, or yellow and blue light act on the retina at the same time and with equal strength they neutralize each other and the sensation of color is completely destroyed. It is difficult to form a clear conception of these processes. Photo-chemical actions of somewhat antagonistic character are well known, but the analogies between them and the visual processes are hardly close enough to be of great assistance.

The hypothesis, however difficult to conceive of in itself, is very definite, and explains as well as the Young-Helmholtz theory the results of ordinary color-vision, and in respect to subjective phenomena, as contrast, or after-images, is much more satisfactory, in formal statements at least. But it fails equally, though for different reasons, to explain satisfactorily the more lately discovered or less evident phenomena of vision.

Complementary colors are regarded, on this theory, as mutually destructive, the one representing an assimilative, the other a dissimilative process. The white or grav which results from their combination is due to the action on the white-black visual substance, which was unperceived in the separate colors, being masked by their greater brilliancy, but becomes effective when they are neutralized by mixture. If two equal grays are formed, one let us say from red and green, the other from yellow and blue, they must according to the theory contain equal amounts of white, and the colors in each are completely neutralized. Thev should, therefore, remain equal at all degrees of brightness. But Ebbinghaus,* by mixing spectral colors, and Mrs. Franklin, + with color-disks, have shown that this is not true. If they are made equal when bright, and the intensity gradually diminished, the red-green mixture greatly exceeds in brightness. If they are equated when of feeble intensity, and then made brighter, the yellow-blue mixture surpasses. Königt has lately examined this with much elaboration, confirming these results, and showing also that the brightness of a gray obtained thus by mixture is always equal to the sum of the brightness of the separate colors, whether by bright or faint light.

This single experiment, so amply confirmed, appears completely destructive to Hering's fundamental hypothesis, at least in its original and simple form.

It may be remarked in passing that photometric methods which have been proposed, of comparing lights of different colors by reducing their brightness until the colordifferences vanish, are worthless.

Other phenomena of similar character exist which are equally difficult of explana-

* Zeitschrift für Psychol. und Physiol. Sinnesorgane, V., p. 145, 1893.

† Mind, N. S., II., p. 487, 1893.

‡ Ber. d. Preuss. Akad., p. 945, 1896.

tion. Hering regards some of these as phenomena of adaptation, and shows, in his remarkable paper on Purkinje's phenomenon, published in 1895, that the state of the retina, as conditioned by previous exposure to light, affects greatly the perception of color. Attention to this fact is necessary in photometric comparisons. The eye should be kept in the same condition, as nearly as possible, throughout any set of observations. But careful measurements by von Kries and others, keeping the eye carefully adapted for brightness, have proved that Purkinje's phenomenon exists, whatever the state of the eye, though much modified by adaptation.

Another cause of false color-appreciation, insisted upon by Hering, is the pigmentation of the macula. This is certainly of importance. In experiments with colordisks the apparatus, to secure consistent results, must always be placed at the same distance from the eye. A color-match made with the disks close to the eyes will in general not hold if the observer steps back a few feet, because the macula covers in the two cases a very different portion of the retinal image of the disks. The region corresponding to the macula, indeed, can generally be seen projected upon the surface of the revolving disks, as a spot inclining more to reddish than the remainder of the surface. The intensity of the yellow pigment, differing in the eyes of different people, must affect their general perception of color.

The well-marked divisions of color-blind, into green-blind and red-blind, as they would be called in the Young-Helmholtz theory, were explained by Hering as due to the more or less deeply pigmented macula. But the utter inadequacy of this explanation has been abundantly shown.

Perhaps the most striking difference between the Hering hypothesis and the facts is shown in the distribution of color-sense in different parts of the retina. Ability to distinguish colors decreases gradually from the center to the exterior. The distinction of red and green disappears first, then the vellow becomes uncertain, and finally blue disappears, the outer zone of the retina being devoid of color-sense. The zones are not well defined, varying with the brightness of the light and the size of the colored surface. But making due allowance for these circumstances, the area within which red is distinguishable differs from that occupied by green, and the yellow sensation differs in extent from the blue. If red and green, or yellow and blue, are due to the presence of the same visual substance it seems that the boundaries should be co-extensive.

Even the sensation of white presents similar variations. There are, as has been already said, three cases in which the colorsense is wanting: the totally color-blind eye, the normal eye in faint light, and the periphery of the retina. The brilliant discovery of Hering, in 1891, that the distribution of brightness in the spectrum in the first two cases is the same, aroused great interest in the theory of the sensation of white, and went far toward establishing its position as a distinct and separate sensation. The third case, it was taken for granted, fell under the same law. But in 1896 yon Kries showed that the distribution of brightness in the spectrum as seen by the outer zone of the retina is different, being practically the same as in the central portion, with its maximum in the yellow, and that the peripheral zone in the retina of a colorblind person shows the same deficient sensation for the longer wave-lengths as in the color-perceiving portion of the eye.

This is a matter of so much interest that I have re-examined it with the flicker photometer, with results differing materially from those of von Kries. According to my experiments, the brightness of the colors of long wave-length diminishes continually, while that of the shorter wave-lengths increases continually, from the center of the visual field to its circumference. The conditions under which von Kries worked, however, were so different from mine that I cannot regard my results so far as necessarily invalidating his. If his results are confirmed, they show that the sensation of white in the normal eye is not completely determined by the twilight sensation, or that of the totally color-blind. It contains elements derived from, or connected with, the mechanism producing the sensation of color, even in those portions of the retina where no color-sensation exists.

I have discussed these two theories somewhat at length, because our growth in knowledge of the facts of color-sensation has been conditioned largely by their existence. The enormous amount of work which has been done on the vision of the. color-blind, on color-vision by varying illumination, on peripheral color-vision, not to mention researches upon more purely subjective phenomena, has been largely suggested by aspects of one or the other of these theories, or undertaken with a view to testing portions of them, and there has seemed no better method exhibiting the results of these researches than by placing them in connection with the hypotheses they were intended to test. I need hardly add that I have been greatly aided in this summing up by the polemical writings emanating from the hostile schools.

In this respect, at least, the two theories have been eminently useful, and have fulfilled one of the chief requirements of a scientific theory—that its explanations can be tested by experiment. The earlier forms of color-theory suggested by Newton and by Young were hardly such. So long as the specific effect was conceived to be entirely in the central organ, to which the nerves merely communicated the vibrations of light, there was little upon which to base experimental work. Helmholtz, by ascribing the specific activity to the nerve-ending itself, made it necessary to describe this activity in some definite way, which could then be tested. The very simplicity of the conceptions of Helmholtz and Hering, at first the apparent guaranty of their truth, has proved their greatest value, but also their greatest difficulty.

It is not to be wondered at that later theorists have attempted to modify one or the other of these hypotheses instead of starting anew. Many such attempts have been made in the last few years, but few have attained more than a passing notice, and none any general acceptance. One or two, however, are of considerable intrinsic interest, and may command attention for a brief period.

Ebbinghaus attempts to advance a step upon the older theories by assigning to a particular retinal substance the function of color-stimulus. He finds this substance in the so-called visual purple, which was studied with great care by Kühne more than twenty years ago. This remarkable substance is reddish purple in its normal condition. On exposure to light it bleaches rapidly, passing through a series of tints until it becomes yellow. On further exposure to light it becomes colorless, but in the dark regains its original purplish tone directly without passing again through the series of changes in color. The color-stimulus is ascribed by Ebbinghaus to the absorption of light by the visual purple, and the character of the light-sensation is directly dependent on the color of the light absorbed, that is, upon the physical properties of the substance.

The purple substance, which is changed by the action of light into the 'visual yellow,'is identified by Ebbinghaus, in its two stages, with the 'yellow-blue' substance of Hering. In its first stage it gives rise to the sensation of yellow, in the second stage to that of blue. The visual purple pertains to that element of the retinal complex known as rods. These are not present in the central portion of the retina, and the visual purple is apparently absent there also. But the fovea is sensitive to blue and yellow, as also to green and red Ebbinghaus supposes that a red-green substance exists, even in the fovea, green in its first stage, red in its second; that the yellow-blue substance exists also in the fovea, but that the two, present there in about equal quantity, and nearly complementary in color, neutralize each other, leaving the fovea colorless. A white-sensitive substance is also supposed to exist, more sensitive to light than any of the colored substances, and thus we arrive at three sets of colorprocesses, similar to those of Hering. The two types of color-blindness are explained by reference to the fact that there are two kinds of visual purple, found in the eyes of different animals, one more relatively red in tone, the other inclining more to violet. The red-blind are supposed to possess one of these, the green-blind the other. Certain anomalous and pathological color-sensations are supposed to be due to disturbances in the conducting nerves or the central organs, and hence need not be fitted into the scheme thus outlined.

The physiological character of this theory, as Mrs. Franklin has shown, can probably not be sustained. It is difficult to believe that such a balance between the visual purple-yellow and the supposed visual redgreen could exist, in all stages of both, that they would remain always complementary, and so the latter always invisible. Yellow light, according to this theory, should be most active upon the visual purple, but, as a matter of fact, this material is bleached very slowly by sodium light, and, indeed, König has shown that its maximum absorption is not in the yellow, but in the green. The visual purple exhibits other striking properties, of which the theory takes no account. It seems probable, on the whole, that the office of this substance is really a very different one, and that if it is concerned at all with vision it is with the sensation of white light, not colored.

The theory of Ebbinghaus, then, if we deny its connection with the visual purple, rests upon the same basis as that of Hering, —a visual substance not identified, perhaps not discoverable, but recognizable only through the precision with which it explains phenomena, and the hypothesis itself becomes in the main a modification of Hering's with the well-known pairs of photochemical substances, modified in their character so as to meet the facts more perfectly, removing some difficulties, but introducing others.

The chief advantage of the hypothesis for explanatory or speculative purposes lies in its greater freedom. The theory of Hering demands six color-processes. These are so connected together that they make not six, but three, independent variables. Ebbinghaus so constructs his substances as to leave them nearly independent, the blue, for instance, no longer serving as the antagonistic substance to the yellow, but regarded as developed out of it, and possessing specific properties of its own. Under certain conditions the color-substances are supposed to neutralize each other, as with Hering, a supposition which adds greatly to the difficulty of the hypothesis; but, in general, five independent variables are at the command of the theorist, which, it is evident, may be endowed with such various properties as to explain almost any conceivable difficulty of color-vision.

It may also be said that, with such an assortment of visual substances at command, the properties of which have at present no known chemical, physical or physiological relations, but are deduced entirely from the sensations dependent upon them, the phenomena might probably be explained in an indefinite number of ways, and the different methods of explanation should be regarded rather as examples of ingenious speculation than as real contributions to the advancement of science.

To such a category belong many of the later theories of vision. They incline to Helmholtz or to Hering according as their point of view is chiefly physical or psychological, for the standpoint of these two theories is fundamentally different.

Helmholtz, showing that all colors can be compounded from three, and that white may be also compounded, assumes that three color-sensations are sufficient, and that white may be regarded as a compound sensation. Hering, relying more upon the direct deliverances of consciousness, denies the compound nature of the sensations of white and of yellow, whatever their physical composition may be, and says explicitly that "the entire separation of the optical nature of a light from the sensation which it arouses in us is one of the most necessary prerequisites to a clear handling of the theory of color." Along the lines of these two theories, then, new hypotheses move, and will move, since each of them stands for something real, and has its own distinct advantages.

Upon a somewhat different basis rests a theory, hardly so much of color as of lightsensation, which was hinted at by various observers, but most clearly worked out by von Kries. This supposes that we possess two entirely distinct kinds of visual apparatus, one dependent upon the cones of the retina, the other upon the rods, and the visual purple connected with them.

Max Schultze, so long ago as 1866, mainly on anatomical grounds, suggested that the rods were probably the most important organs of vision in faint light. Animals which prey by night, as cats, moles, owls, etc., possess retinas rich in rods, but with cones either few or absent. Our own eyes perceive faint light more readily with the peripheral portions of the retina, where rods are numerous, than with the central portions, where they are few.

Helmholtz * pointed out the fact that if the visual purple is actually connected with vision it must have to do with peripheral rather than central vision, since it is absent from the fovea, and suggested that it might have to do with the perception of faint light.

In 1894 König studied the absorption curve of the visual purple, finding it substantially identical with the curve of brightness for the spectrum of low luminosity. von Kries, combining these and other suggestions, considers the visual purple in the rods to be, in the human eye at least, the active agent for the perception of faint light. He shows that the phenomena of adaptation point in the same direction. In strong light the visual purple is soon bleached. An eye 'adapted for brightness' is very deficient in power to perceive faint light. If it is now kept in darkness for about half an hour this faculty is enormously increased. But in about the same period the visual purple is practically restored. The essence of adaptation is the recovery of the visual purple. Red light, which does not act upon this substance, does not destroy the sensitiveness to faint light in an eye which has been exposed to it for even a considerable time.

If vision by faint light depends, wholly or partly, on the decomposition of the visual purple, and if light of long wave-lengths does not effect this decomposition, blue light when faint should appear much brighter than red, and Purkinje's phenomenon is thus easily explained. But in the fovea, where the rods and the purple are not present, this sensation of colorless faint light

* Physiol. Optik, 2d. ed., p. 268.

should not exist, and the color of any light bright enough to affect this portion of the retina at all will at once be recognized. von Kries declares this to be a fact. Two colors, equally bright in strong light, will remain so at all illuminations if their image falls entirely on the fovea; but, if not, the color which is of the shorter wave-length will in general be the brighter.

Vision by strong light, and color-vision, since both are possessed by the fovea, must be effected by the mechanisms of that retinal area, and these sensations von Kries attributes to the cones, which are supposed to be furnished with a tri-chromatic colorapparatus, and to afford the sensations of color and a compound sensation of white. If objection is made to the compound white the details of this latter apparatus might be varied, might even approximate that of Hering's theory, without affecting the importance of the hypothesis, the essence of which is the twofold nature of the sensation of brightness.

Such a theory explains easily the fact that grays compounded from different pairs of complementary colors, and equally bright in ordinary light, cease to be so in faint light. They are equalized at first by the cone-apparatus, and are seen in the faint light chiefly by the rod-apparatus, in which the scale of brightness is entirely different.

G. E. Müller makes the acute suggestion that the visual purple may not be a visual substance at all, properly speaking; but, while concerned chiefly with the phenomena of adaptation, may act also as a *sensibilisator* —to borrow a photographic term—for the white-sensitive substance, increasing its susceptibility in faint light. This modification of von Kries' hypothesis is perhaps simpler than the original and equally satisfactory.

Still another hypothesis for separating the white from the color-sensations is that the sensation of white, from an evolutionary standpoint, was developed earlier than the sensations of color, and that the mechanisms of the latter are to be regarded as evolved from that of the fundamental sensation, and as modifications of it. Upon this idea Mrs. Franklin has founded her ingenious theory of light-sensation. Abney has made a similar suggestion, but in general terms only.

Such is a brief and hasty summary of the progress of color-theory. We may well ask for the result. In the general shifting, what views have maintained or gained a footing? A few, I think, are fairly well established.

The number of color-sensations is 1. small, and all color-theories positing a large number are to be distrusted. If experimental work is of any value whatever, it is certain that all light-sensations, for all purposes, may be expressed by a small number of variables. The Young-Helmholtz theory demands three. Hering's requirements, as Helmholtz has shown, may be expressed in terms of three, although the number of fundamental color-sensations, using color in its ordinary sense, is four. Such theories as those of von Kries and Mrs. Franklin require four variables, such as that of Ebbinghaus five. The introduction of a much larger number is gratuitous and unnecessary.

2. Out of this number of variables at least one is to be alloted to the whitesensation, or that which is closely akin to it, the sensation of brightness. It is no longer possible to think of white entirely as a compound sensation, however it may be compounded physically. It is unnecessary to recapitulate the arguments for this statement, drawn largely from the three forms of total color-blindness.

3. White, however, can hardly be thought of as an entirely independent sensation. The phenomena of vision by faint light, the facts of peripheral vision, show that, under certain circumstances, color-sensations contribute their quota to the colorless one, and in differing amounts at differing brightness. These phenomena are not satisfactorily handled by any of the principal theories. They are fairly well explained by the Helmholtz suggestion of shifting color-curves, nearly as well by the hypothesis of Hering and Hillebrand, that color-sensations possess specific brightening or darkening power, which makes itself more notable as the intensity increases. These are but formal explanations, however, and increase rather than diminish the difficulties of the theories to which they are attached.

4. The theory of von Kries, of different visual mechanisms for bright and faint light, supplements excellently the existing theories, and must be regarded as a distinct step in advance.

5. A definite and highly probable function has been assigned to the visual purple, the function of adaptation, and of causing or aiding vision in faint light.

Farther than these at present we can hardly go. The number and variety of known phenomena are great and constantly increasing. Their inter-relations grow every day more complex, and the actual mechanism governing those relations still remains almost entirely unknown. Subjective experiment appears likely to yield little more aid. The various theories have arrived at such a state of perfection, and, thanks to subsidiary hypothesis, to such a state of flexibility, that almost any visual result might probably be explainable by either. Perhaps the most hopeful line of research is that which, like König's study of the visual purple, seeks to find some relation between color-sensations and physical properties. Since so many phenomena point to photo chemical changes in the eye, it would not be surprising if the next advance should come from the chemical side. rather than from the physiological, physical or psychological, which have held the field so long. FRANK P. WHITMAN. ADELBERT COLLEGE.

A HALF-CENTURY OF EVOLUTION, WITH SPECIAL REFERENCE TO THE EFFECTS OF GEOLOGICAL CHANGES ON ANI-MAL LIFE (III.).*

4. THE UPPER CRETACEOUS REVOLUTION.

ANOTHER profound and epoch-making change occurred at the beginning of the Upper Cretaceous. In Eurasia, as Kayser states, "this was one of the greatest changes in the distribution of land and water over almost the whole earth that is known in geographical history. Extensive areas which had for long periods been continents were now overflowed by the sea and covered with Cretaceous deposits;" the Upper Cretaceous strata in certain areas in Germany and Belgium resting directly on archean rocks. In America (the Dakota stage) there was also a great subsidence. The Atlantic coastal plain was submerged over what was Triassic soil, also the lowlands from New Jersey through Maryland to Florida, while the Gulf of Mexico extended northward and covered western Tennessee, Kentucky and southern Illinois; a wide sea connected the Gulf of Mexico with the Arctic Ocean, and thus the North America of that time was divided into a Pacific and an Atlantic land. the latter comprising the Precambrian and Paleozoic areas.

As Scott states: "The Appalachian mountains, which had been subjected to the long-continued denudation of Triassic, Jurassic and Lower Cretaceous times, were now reduced nearly to base-level, the Kittatinny plain of geographers. The peneplain was low and flat, covering the whole Appalachian region, and the only high hills upon it were the mountains of western North Carolina, then much lower than now. Across this low plain the Delaware, Susquehanna and Potomac must have held very

^{*}Address of the Vice-President before Section F— Zoology—of the American Association for the Advancement of Science, August, 1898; concluded from SCIENCE, September 2d.