Summary

On Young's hypothesis, a simple explanation can be advanced for the fact that both the red and the green blind call the less refrangible end (long wave length end) of the spectrum yellow, namely, that they have found by experience that their long wave length sensation is most strongly aroused by objects which the normal sighted call yellow. This also explains why they call greens, both spectral and pigmentary, dirty yellow, grey, or grey-blue according to shade. Also why they call white "white" and not purple, on the one hand, (green blind) or blue green, on the other (red blind).

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DR. EDRIDGE-GREEN'S THEORIES OF VISION

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DR. EDRIDGE-GREEN, in his many writings on colour vision and kindred topics, has advanced several theories. He has been indefatigable in his attempts to support these theories by statements based upon, and criticisms directed against, the work of other investigators, as well as by extensive series of observations of his own. It is not unnatural that in his enthusiastic advocacy of his views he should appear at times somewhat to underrate the work of his predecessors and contemporaries in the same scientific field. The sole object of the following remarks is in some measure to restore the balance. In my opinion, the time is not yet ripe for dogmatic allegiance to any of the many theories which have been propounded to explain the phenomena of colour vision. In my "Introduction to the Study of Colour Vision" (1915, Cambridge University Press) I have briefly described and criticized the chief theories, including Dr. Edridge-Green's. The value of a scientific theory depends not only upon its capacity to elicit useful generalizations from established facts, but also to stimulate the imagination to devise new methods of attack. In the latter respect is its utility chiefly to be judged, and therein lies the criterion which distinguishes it from vague speculations.

1.—The Function of the Rods

Dr. Edridge-Green says: "The rods are not perceptive elements." ("The Physiology of Vision," p. 134).

Some of the evidence in favour of the rods being perceptive elements is as follows:

1. *Comparative Anatomy*.—In most mammals, amphibia, and fishes, there are rods and cones, the former being the more numerous; in birds the cones are more numerous than the rods. In most reptiles (lizards, snakes, and tortoises) only cones are found. There are vertebrates possessing only rods, e.g., among fishes, rays, and dog-fish: among mammals, hedgehogs, bats, mole, and night ape (*Nyctipithecus felinus*). There are also animals of nocturnal habits possessing only rods. Owls, mice, and rell-mice have only a few rudimentary cones; rats also have a few cones.

The fact that there are seeing animals which possess only rods negatives Dr. Edridge-Green's statement. The fact that there are seeing animals which possess only cones proves that Dr. Edridge-Green's theory of the photochemical activation of the cones by visual purple secreted by the rods is not true for these animals.

2. *The Colourless Interval*.—If the eye is dark-adapted lights of low intensity from all parts of the spectrum, if seen at all, appear colourless. As the intensity is increased colour is seen, first for light of long wave-length (red) and at greater intensities for lights of shorter wave-length. The photo-chromatic interval is much diminished, if not, as held by many competent observers, entirely absent from the fovea. It is greater for the peripheral than for the paramacular region of the retina. It is probable, therefore, that the cones are insentitive to low intensities of light in the dark-adapted eye and are concerned, inter alia, specially with photopic or colour perceiving vision, and that the rods are specially sensitive to low intensities of light in the dark-adapted eye and are concerned specially with scotopic or achromatic vision.

3. *The Purkinje Phenomenon*.—With diminishing intensity of light and increasing dark adaptation the brightness of different coloured objects alters, the colours towards the red end of the spectrum becoming relatively darker, those towards the violet end brighter, so that finally the reds appear almost black and the blues white. In the colourless spectrum of light of low intensity seen by the dark-adapted eye the brightest part is at about $530\ \mu\mu$, i.e., the part which seen with higher intensities is green, and the blue end is sixteen times as bright as the red end. In the spectrum of higher intensity seen by the light-adapted eye the brightest part is at about $580\ \mu\mu$, i.e., in the yellow, and the red appears about ten times as bright as the blue. Although there is some difference of

opinion on the point, most competent observers (*e.g.*, König, Lummer, Nagel, v. Kries, and others), using the most refined methods, agree that Purkinje's phenomenon is absent at the fovea.

Purkinje's phenomenon strongly supports the view that two different mechanisms are at work in scotopic and photopic vision, the former being carried out by the rods, the latter by the cones (plus or minus the rods). The absence of the phenomenon at the fovea supports the view that the cones play no part in scotopic vision.

(4) *The Absorption of Monochromatic Light by the Visual Purple.*—The curve of absorption of monochromatic lights by the visual purple is almost identical with the luminosity curve of the achromatic scotopic spectrum, *e.g.* the point of greatest absorption is at about $530\text{ }\mu\mu$, which is the brightest part of the colourless spectrum of low intensity as seen by the dark-adapted eye. Now the visual purple is found only in the rods. Hence it is justifiable to conclude that the rods and visual purple are specially concerned with scotopic vision.

(5) *Reversed Purkinje Effect.*—There can be no doubt that the visual purple is of fundamental importance in scotopic vision and that its accumulation is the basis of dark-adaptation. It follows that the relation of the achromatic scotopic luminosity values of two lights, *e.g.*, a green which is strongly absorbed and an orange which is weakly absorbed by the visual purple, should depend upon the concentration of the visual purple in the rods, *i.e.*, it should vary with the degree of dark adaptation. Stegmann has shown that such is the case. If a luminosity match is made between green and orange with intensities at which they appear colourless after 5-15 minutes' dark adaptation, and the lights are again compared after much more prolonged adaptation the orange appears much brighter and must be diminished to about three-quarters of its former intensity to restore the match.

(6) *Pupil Reactions and Electrical Responses.*—Sachs showed that the pupil-reactions vary with the luminosities of the lights, independently of their colour, both in the normal and the colour-blind. Abelsdorff confirmed these observations and showed further that maximum pupil-constriction occurs in nocturnal animals from green light, whereas in animals of diurnal habits the maximum is obtained from yellow-light.

Similar, but more reliable and much more striking results, have been obtained from the electrical reactions, especially in day- and night-birds by Himstedth and Nagel, and Piper.

(7) *Photopic and Scotopic Colour Matches.*—The changes in the value of colour matches, formerly referred to as "deviations from Newton's law of colour mixtures," on altering the intensity of the light and the state of dark adaptation are explained by the theory

that the photopic values are cone-values, those at lower intensities rod- and cone-values mixed, and those at the lowest, rod-values. Thus, Albert showed that spectral yellow matched with a suitable mixture of red and green ceased to match on diminishing the intensity, and Ebbinghaus and Mrs. Ladd-Franklin showed that "three whites made by mixture of red and blue-green, yellow and blue, and green-yellow and violet darken unequally with proportionally diminishing intensity, the first least, the second more, and the third most." In general, matches valid for high intensities become invalid for low intensities and dark adaptation in the sense that the mixture which possesses the greater rod-value exhibits the greater luminosity in tone-free scotopic vision (v. Kries).

(8) *Visual Acuity*.—König, in 1897, made a very accurate series of observations on visual acuity with white and monochromatic lights. If the intensities of illumination are plotted as abscissae on a logarithmic scale and the visual acuities as ordinates the curve is a straight line of gentle slope up to 0.25 metre candle illumination. There is then a sharp bend and the curve becomes a straight line of much steeper slope up to the maximum. The same type of curve is seen with red, green, and blue light, but with red light the preliminary slowly rising part is very short. König himself drew the conclusion that two different elements of the percipient layer of the retina are involved, and that under low intensities of light vision is due to the activity of the rods, under higher intensities to that of the cones.

(9) *Critical Frequency*.—When two lights of different brightness, whether of the same or of different colours, are alternated flickering is observed. If the rate of alternation is gradually increased a "critical frequency" is ultimately reached at which the flickering disappears. The flicker phenomenon is dependent entirely upon the brightness of the lights and not upon their colour. T. C. Porter found that the relation between the intensity of illumination and the number of revolutions per minute at which a disc, half white and half black, must be run in order that the flicker may just disappear follows a definite mathematical law. If the rapidity of stimulation increases in arithmetical proportion, the intensity of illumination must increase in geometrical proportion in order that flicker may be avoided. Expressed in the form of an equation, $n = k \log I + k'$, where n is the number of revolutions, I , the intensity of the light, and k and k' , two constants. This relation was found rigidly true for illuminations from 0.25 metre candle to 12,800 times this value. But the remarkable fact was elicited that below 0.25 metre candle, the constant k suddenly changed its value to about half its former value. These results have been confirmed by Ives, Dow, and many others. The change is exactly parallel to that found by König for visual acuity. It occurs at the same intensity, about 0.25 metre candle, and is almost universally attributed to the same cause, viz.,

that below 0.25 metre candle the rods are the percipient mechanism, above that value the cones.

(10) *Total Colour Blindness*.—There are cases of congenital total colour blindness, in which light is perceived but no colours. In these cases it is found that the brightness values of spectral lights correspond exactly with those of the normal dark-adapted eye stimulated by lights of low intensity. Comparison of the luminosity curves shows their almost complete identity. Whereas, however, the normal achromatic scotopic curve is valid only for low intensities of objective lights the achromatic curve is valid for all intensities, though with the higher intensities photophobia occurs. The process of dark adaptation pursues the normal course in the totally colour blind. Exposure to bright light causes prolonged diminution of vision, and recovery follows the course which would be expected if it were dependent upon restoration of the visual purple.

All totally colour blind people have marked diminution of central visual acuity, and in many cases there is undoubtedly a central scotoma. The curve of visual acuity with gradually increasing light-intensities shows no sudden bend, as in normal-sighted people, but continues in the same direction as for lower intensities until photophobia sets in (König). The reduction in central vision tends to absence of binocular fixation and divergence of the optic axes. We may conclude that the foveal neuroepithelium, if it retains its function at all, approximates in character to that of the normal rods.

Uhthoff and von Kries have shown that the flicker phenomenon in the totally colour blind follows the same laws as in normal achromatic scotopia.

The simplest explanation of these cases is that cone vision is almost entirely, if not entirely, in abeyance, and that vision is carried out by means of the rods.

(11) *Night Blindness*.—Night blindness is found in several diseases of the eye, most commonly in retinitis pigmentosa and allied conditions, least adulterated by other pathological symptoms and signs in congenital night blindness. The last-named is congenital and hereditary.

In night blindness dark adaptation may be almost abolished or much slower than normal; in high degrees it is both slowed, and diminished quantitatively, i.e., the higher degrees of sensitiveness of the retina are never reached and the highest possible are reached only after prolonged exclusion of light from the eye. In low degrees central vision is normal in the light-adapted condition, and may be so in high degrees of the disease, e.g., in retinitis pigmentosa. Colour vision is normal with the exception of occasional diminution of sensibility for blue lights. In retinitis pigmentosa the field of vision is diminished, often almost down to the fixation point, and dark adaptation may be completely absent.

Purkinje's phenomenon is much less marked in the night blind. If a red and green are chosen, which are equal in luminosity for the normal and night blind in light adaptation, and the room is then darkened, the green then becomes much brighter than the red in the course of a few minutes for the normal, but only after a long time, if at all, for the night blind. Quantitative experiments show that for lights of short wave-length the increase in luminosity after half-an-hour's dark adaptation is 10 to 100 times as great for the normal as for the night blind. With stimulation areas exceeding the foveal limits the sensibility for mixed white lights increases much more rapidly for the normal than for the night-blind on dark adaptation, but if both are tested with red lights there is very little difference. This is further proof of the diminution in the appreciation of Purkinje's phenomenon by the night blind.

The simplest explanation of these cases is that in them rod-vision is seriously disturbed or in abeyance. The pathology of retinitis pigmentosa supports this view. This disease is primarily due to vascular degeneration in the choroid, whereby the chorio-capillaris is destroyed. The pigment epithelium and the outer layers of the retina are dependent for their nutrition upon the integrity of the chorio-capillaris. From its proximity the pigment epithelium must suffer first. The production of visual purple in the rods is undoubtedly bound up in the integrity of the pigmented epithelial cells, so that primary disorder of the functions of the rods might be confidently anticipated on pathological-anatomical grounds. It is the rule in most nutritional disorders for the most highly differentiated and complex structures to suffer first. That there is good evidence of a survival of the cone-functions after destruction of rod-functions is evidence of an intermediary process such as that described.

12. *Anatomical Structure and Evolution.*—It seems almost inconceivable that two structures so similar in form and composition, in position and anatomical relations, should have such diverse functions as are attributed to them by Dr. Edridge-Green. Even in the human retina intermediate forms are seen of such a nature that it is difficult to determine whether they are really rods or cones, and in the fovea itself the cones are elongated and cylindrical, resembling rods more closely than elsewhere. Of the two the cones are the more complex in structure and the rods are absent at the most highly differentiated part of the retina. The natural conclusion, which is supported by analogy and by comparative anatomy, is that the rods are the more primitive visual element, and that the cones have become differentiated from them in the course of evolution. It is consistent with this view that the rods retain in man the primitive function of mere light perception, whereas the more highly differentiated cones have acquired the

more complex function of responding specifically to qualitative varieties of light stimulus. Yet they too retain the capacity to respond to the unanalysed light stimulus, a good example of what I have elsewhere in this Journal described as the apocritic principle of the evolution of perceptions.

Moreover, as Sherrington has pointed out, Dr. Edridge-Green's hypothesis as by the rods leaves unexplained their linkage to the retino-optic nerve-paths. It denies to one half—in some animals to much more than a half—of the optic nerve fibres the conduction of visual impulses. It makes difficult the attribution to these fibres of any afferent function.

Taken literally, Dr. Edridge-Green's statement that Nagel says "There is also not a single fact pointing to the view that the rods are percipient elements" is true. It is, however, misleading. The passage referred to is as follows:

"What has been said above (referring to the exact site of retinal stimulation) speaks only in favour of the cones, but not of the rods, as light-perceiving elements, and there is indeed nothing against the view that the latter remain passive in actual seeing, as amongst others was conjectured by Gad, who regarded the rods as elements concerned in reflexes. Two kinds of end apparatus of clearly different structure, which nevertheless possess the same function, must also give rise to doubts. These may, however, be regarded as eliminated, since the theory first propounded by M. Schultze and brought to the highest degree of probability by Parinaud and von Kries has rendered it possible to consider the rods as well as the cones as light-perceiving elements, and to account for the differences in structure of the two organs and the differences in their connection with the optic nerves by the suggestion of essentially different functions."

The arguments which have been gathered together above are the chief arguments in favour of the theory referred to by Nagel, generally known by the name given to it by von Kries, the Duplicity Theory. Like most generalizations of this kind it fails to account satisfactorily for all the facts. The phenomena of peripheral vision are difficult to reconcile with it, and Siven has collected other arguments against it. Dr. Edridge-Green, however, is probably the only worker in this field who denies *any* light-perceiving function to the rods.

II.—The Photo-Chemical Theory

Since Boll, in 1876, discovered that the visual purple was bleached by exposure to light, and more especially since Kühne's exhaustive investigations, a photo-chemical explanation of the action of light on the retina has been the most popular. Kühne found visual purple in the rods only, and this observation has been

confirmed and is generally accepted. Dr. Edridge-Green holds that the substance diffuses into the surrounding fluid and becomes distributed to every part of the outer layer of the retina. He found it between, and not in, the cones of the fovea. Hering has already suggested that visual purple may not be wholly absent from the cones, and the peculiar rod-like character of the human foveal cones makes it not improbable that they contain some of the substance. This would account for the (feeble) dark adaptation of the fovea. Dr. Edridge-Green has described in detail "currents seen in the field of vision not due to the circulation," and attributes them to movements of the fluid activated by the visual purple.

It does not *a priori* appear at all probable that vision depends upon the wide-spread diffusion of sensitized molecules in a fluid medium. If it were, it would be very difficult to understand how the extremely fine discrimination of minute objects, e.g., a visual acuity with a minimum visual angle considerably less than one minute, such as is often met with, could be obtained. It is far more probable that if the process is photo-chemical the reaction takes place in the neuro-epithelium itself. Possibly this is what Dr. Edridge-Green really means; but if so, it seems inconsistent with his explanation of the shifting and breaking up of after-images by shaking the head. It is surely unlikely, on physical grounds, that fluid filling the minute interstices between rods, cones, and pigment epithelium, should be shifted and scattered by merely shaking the head.

It is also improbable that the fovea, the part of the retina which is most sensitive in photopic vision, and which is specially differentiated for the discrimination of minute details, should be sensitised by fluid flowing along definite channels from the surrounding areas. The anatomical evidence in favour of such channels is of little value. Such as is derived from gross pathological lesions, like Sir Victor Horsley's case of choked disc with a macular star-figure in a case of intracranial tumour, is, in my opinion, valueless. This condition nearly resembles that found in albuminuric neuroretinitis; it is due to oedema of the retina, with abnormal exudates which so disturb the normal relations of the parts that evidence derived from it as to the normal structure is more than usually untrustworthy.

Burch, in 1913 (*Proc. Roy. Soc.*, B 86, p. 490), says, "Every hypothesis, whether mechanical, photo-chemical, or ionic, concerning the connection between the light-waves and the sensations they evoke, must of necessity rest ultimately on the theory of forced vibrations." Discussing the opto-chemical processes mathematically on this theory he derives four hypothetical colour-sensation curves, which meet the requirements of colour-mixtures and colour-

fatigue, on the same principle as the Young-Helmholtz theory, as modified by Burch himself. By altering the coefficient of friction he finds that the now flattened and extended curves explain the colourless scotopic spectrum. He then discusses the physiological elements of the visual sensation, and finds it necessary to hypothecate a "shunt-factor" whereby the strength of the sensation is governed. Otherwise "the theory of forced vibrations would indicate that with intense and long-continued illumination the several colour sensations must stand out more and more distinctly instead of becoming paler and tending towards white."

The theory of forced vibrations as applied to colour vision has been further elaborated in a paper by Houstoun (*Proc. Roy. Soc.*, A 92, 1916, p. 424). By making subsidiary assumptions, Houstoun, like Burch, is able to bring the theory into line with the Weber-Fechner Law, and also to explain the achromatic scotopic spectrum. He concludes that it is not necessary to assume two different mechanisms, and that "there is no decided evidence in favour of three classes of vibrators."

I am not competent to criticize the mathematics of forced vibrations. It appears that this theory supports Dr. Edridge-Green's theory of a single mechanism for both photopic and scotopic vision, if a further assumption is made. This assumption, if justified, must be pitted against the many arguments which I have adduced above in favour of two mechanisms.

Houstoun apparently does not find it necessary to resort to the shunt factor of Burch. Monochromatic light becomes whiter at high intensities because "when the impressed force on the vibrator is increased, the latter is more strongly damped, and hence the energy of the Fourier components of its motion more widely distributed over the spectrum."

While Houstoun considers that "the reception of light by the eye can be represented broadly by one class of vibrators," Burch's exposition shows that the three (or four) components theory is consistent with the theory of forced vibrations. On the principle, *simplex sigillum veri*, Houstoun's view is the more acceptable, *unless* the phenomena are more easily explained by the more complex view. There is some reason to think that this is the case. For example, Houstoun finds it necessary to invoke Dr. Edridge-Green's theory that "the colour perceiving centre in the brain is not sufficiently developed to discriminate between the character of adjacent curves" in order to explain the apparent trichromatism of our ordinary sensations.

Moreover, as Burch (*Ophthalmoscope*, Vol. X, 1912, p. 57) pointed out in a criticism of Dr. Edridge-Green's view that the character of the stimulus differs according to the wave-length of the light to which it is due, and the discrimination of these differences is

a function of the brain, this hypothesis is directly opposed to the law of the specific energy of the senses. This law has been much discussed and is not universally accepted, but since Dr. Edridge-Green cites it with approval "(Physiology of Vision," p. 1) the argument should have some weight with him.

Probably most competent judges will agree that the light stimulus is of a photo-chemical nature and that the physical basis is one of molecular forced vibrations. They will, however, suspend judgment as to the exact details of the mechanism.

(To be continued).

ANNOTATIONS

Compulsory training and examination in Ophthalmology

During the past two years the General Medical Council has been urged to compel all medical students to study ophthalmology and to have them examined by specialists before they receive a licence to practise. Ophthalmic surgeons are so convinced of the necessity of this measure that the Oxford Ophthalmological Congress, the Council of British Ophthalmologists, and the Ophthalmological Society of the United Kingdom passed unanimous resolutions which have been considered by the General Medical Council. At the recent Congress of the Ophthalmological Society, the President, Mr. J. B. Story, P.R.C.S.I., devoted his opening address entirely to this question. He regretted that the General Medical Council had refused to institute a formal examination in diseases of the eye and had only consented to ask for some evidence of practical training in the subject. He pointed out that it was essential for every medical practitioner to possess a working knowledge of ophthalmology, and for two reasons: because rarely can a qualified man escape the necessity of treating eye patients at some time in his career, and secondly, the evidence afforded by an examination of the eye is needed for the diagnosis of many ordinary medical diseases; in fact, it has been stated that the ophthalmoscope is as essential as the stethoscope.

The General Medical Council had, he said, come to no logical conclusion, and had virtually tried to shift the responsibility on to the Hospital Medical Schools, who are empowered to refuse certificates to students who do not acquire a sufficient knowledge of eye diseases. The President reminded the Society that all the Irish licensing bodies had held a special clinical examination, and that this fact disposed of the objection that there was no time for