RECENT ADVANCES IN THE PHYSIOLOGY OF VISION—PART II*

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When Young's three-colour theory was first put forward by its celebrated proposer it dealt adequately with all the facts of colour vision which were known at that time. It stated that all colours, including white, can be matched by suitable mixtures of three spectral primary colours—red, green, and blue. As methods of investigation improved and the scope of the inquiry widened, deficiencies in the theory began to disclose themselves. Thus Sir John Parsons (1924a) wrote: "Difficulty is experienced when an attempt is made to explain the phenomenon of peripheral vision, or of induction, by the theory." Recognition of this difficulty did not cause the abandonment of the theory, because it still had much to recommend it; it was easily understood; it provided a useful classification of the various types of colour-blindness; it offered a feasible explanation of many visual phenomena, and it was an incentive to further research. By degrees, however, its position has deteriorated with the acquisition of further knowledge, in which connexion special reference should be made to Granit's work (1943, 1945), in which he applied the micro-electrode technique to the retinae of many mammals. He did not find that there were three types of colour receptor, as would have been expected on the basis of Young's theory—namely, red, green, and blue—but as many as seven in the frog and four in the cat. These researches, which I reviewed last year (Hartridge, 1946a), were a serious setback to Young's theory, which had held the field for more than a century.

Section I: Retinal Micro-stimulation

When Granit's researches on animals were published I began to look for a method which would be applicable to an intact man. In the case of an animal the cornea, lens, and vitreous may be removed, and the electrode placed direct on the individual fibres of the optic nerve as they pass across the surface of the retina to leave the eyeball at the optic papilla. In the case of man, except under unusual conditions—where the eyeball has been seriously injured as the result of an accident, or where it is to be removed for medical reasons—Granit's method cannot be applied, and therefore a different principle has to be used. The plan I finally adopted (Hartridge, 1947) was to apply to chosen parts of the retina pencils of white or coloured light which were so narrow that they stimulated small groups of receptors, or even, under good conditions, single receptors. These tenuous beams of light were produced by a lens system of special design which resembled a microscope used the reverse way round. Whereas the latter magnifies, the micro-stimulator lens system diminishes the images of small sources of white, or of monochromatic, lights until they become mere pin-points. Their geometrical images subtend at the eye an angle of 8 seconds of arc, and they form on the retina geometrical images whose diameters are equal to one-fifth of a cone unit.

Before using the instrument care was taken to correct as perfectly as possible defects present in the lens system of the observer's eyes. As a rule only one eye was used at a time. This instrument gave satisfactory results and was employed for studying a number of different problems. Three concern us here: (a) to determine whether there is a constant fixation-point in the fovea for light of any given colour and brightness, or whether different fixation-points are used at different times; (b) to determine whether lights of different colour use the same or different fixation-points; and (c) to ascertain which colours, if any, are to be seen when a tiny ray of white light is caused to explore the surface of the retina.

(a) The position of the fixation-point for green rays (5,200 A.U.), was determined in relation to a small scotoma for red rays which existed near the fovea, in my left eye (Hartridge, 1946b). The precise position of the fixation-point was measured a number of times, on three different evenings, and was found to alter hardly at all in position. The greatest difference between the three mean values was found to be less than one-quarter cone unit.

(b) When rays of other colours were similarly tested it was found that each colour had a definite fixation-point of its own. In all, seven different points were located—namely, for red, orange, yellow, green, blue-green, greenish blue, and blue. The red and the orange fixation-points were to the left and below the green ones; the yellow, the green, and the blue-green points were all close to one another; while the greenish blue and the blue points were to the right and below the green ones in the visual field. These positions were confirmed by another method, so far as red, green, and blue were concerned, which involved the estimation of eye movements required in order to fix, in turn, first one of these coloured points, and then another.

(c) With regard to the third type of experiment, it was found that a beam of white light remained white in appearance, wherever it was situated on the retina, unless there was also present a conditioning coloured light in the visual field. When this was the case colour changes were found to occur. Thus when the conditioning coloured light was red the white light looked white in certain positions but red and orange in others. Examined in this way the white light was seen on different occasions to have the following subjective colours: red, orange, green, blue-green, greenish blue, or blue. Yellow was also seen under advantageous conditions; making seven colours in all.

Thus by means of two different methods—the fixation method and the subjective colour method—evidence was found for the presence in the human fovea of several different kinds of receptor. Now, such methods may give fallacious results unless great caution is exercised by the observer in their performance and interpretation. In consequence it would have been unwise to place reliance on them unless they had been confirmed by the other methods, which are described in the following sections.

Section II: Colour Mixture Experiments

With the apparatus available to Thomas Young and his contemporaries it seemed possible to match exactly the monochromatic yellow light of the spectrum by a suit-

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able mixture of spectral red and spectral green lights. As spectroscopic apparatus improved, so as to produce purer spectra and to permit more exact comparisons to be made, it was found that a precise match was not obtained, because the monochromatic yellow was always more saturated—that is, contained less white light—than the yellow produced by mixing red and green. Thus for equality to be obtained either white or, better, blue light was mixed with the pure yellow. In the case of the blue-green colours it was red light which was added for the same purpose. In the case of the red or the violet, near the ends of the spectrum, it was green light which was required. Now, adding a colour to one side of a match is equivalent to subtracting it from the opposite side. The colour equations therefore took this form:

- (a) Extreme red = red + blue – green
- (b) Yellow = red + green – blue
- (c) Blue-green = green + blue – red
- (d) Extreme violet = red + blue – green

These negative amounts of red, green, and blue were accounted for in various ways. Thus Wright (1946a) states: "All it means is that no physical radiation is capable of stimulating one of the receptor systems without causing activity in the other systems." This may be restated: "A red light stimulates the red receptors, but also to some extent the green ones and the blue ones, and similarly for lights of other colours." Göthlin (1943) held a different opinion, and thought that cerebral inhibition accounted for these negative values. At present there is no confirmatory evidence for either of these views.

Whatever the cause of the negative values may be there is no doubt that subtracting a given colour is equivalent to the addition of its complementary. Thus the subtraction of red is equivalent to the addition of blue-green, the subtraction of blue equals the addition of yellow, and the subtraction of green equals the addition of both extreme red and extreme violet.

The four equations given above therefore become:

- (a) Extreme red = red + blue + extreme red + extreme violet
- (b) Yellow = red + green + yellow
- (c) Blue-green = green + blue + blue-green
- (d) Extreme violet = red + blue + extreme red + extreme violet

On the left-hand side are all the colours of the spectrum, of which red, yellow, blue-green, and violet have been taken as examples. On the right-hand side are the spectral components required to match them. The latter comprise the following colours: extreme red, red, yellow, green, blue-green, blue, and extreme violet; seven colours in all.

Section III: Colour-blindness

It used to be thought that there were four kinds of defective colour-vision—red-blindness, green-blindness, blue-blindness, and total colour-blindness—and that the first three were due to the failure of one type of receptor, while the last was caused by a complete breakdown of all three types.

Such a classification fitted in with the three-colour theory and lent it very strong support. Soon, as the result of research, further varieties of colour deficiency came to light. In addition to the red-blind (protanopic) there were also the red-deficient (protanomalous); in addition to the green-blind (deuteranopic) there were the green-deficient (deuteranomalous), and so on. Then it was found that there were various grades of failure of vision for the red rays: in some cases it was the red near the end of the spectrum only that was involved; in other cases it was the whole of the red; in still other cases the red and the orange were affected together, and so on. In order to account adequately for all these different grades the red sensation

had to be supposed to consist of several separate parts, each one of which could become deficient by itself or in conjunction with other parts. In the case of green-blindness also, changes of mechanism had to be introduced, and the original idea of a partial or a complete deficiency had to be replaced by a different plan altogether proposed by Pitt (1944)—namely, a partial, or a complete, linking of the red receptors with the green ones. So with blue-blindness it is no longer regarded as a defect of the blue receptors, as was once the case, but as being due to absorption of blue rays either by some yellow pigment in the crystalline lens or in the retina (Parsons, 1924b). Thus the original simple arrangement, which appeared to support the three-colour theory so strongly, has gone, for not one of the types of colour-blindness is believed to-day to be caused by the absence of a single sensation mediated by a particular type of receptor. Thus Young's original theory can no longer look to colour-blindness for support, as it once could. In order to come into line with the facts of colour-blindness as we now know them, the red receptor has to be regarded, as Wright (1946b) has pointed out, as being a composite affair, consisting of several different types of receptor—some for red rays, some for orange rays, some perhaps for yellow rays—interconnected in some way in order to mediate the red sensation. Hence Young's theory has been forced to adopt polychromatism in order to account for colour-blindness.

Section IV: The Inconstancy of the Receptor Curves

In the early days of the colour theories it was usual to deal with sensations. Accordingly, Young's theory supposed that to each primary colour there was a corresponding sensation. Thus red light, incident on an active retina, caused under suitable conditions a red sensation to be perceived, and so on for green and blue. Nowadays, in keeping with the times, we prefer to think in terms of the photo-receptors present in the retina, and by carefully planned experiments we try to determine their sensitivity to different parts of the spectrum; this is plotted against wave-length, thus producing what is called a "response curve." If the response curves derived by the different methods resembled one another exactly it would be very encouraging to Young's theory. But such is a long way from being the case, so far as present evidence is concerned. The red receptor is particularly unfortunate in this respect, for when deduced from the colour mixture equations it has a smooth curve, rising to a single crest at about 5,800 A.U. (Fig. 1). When, on the other hand, it was deduced by Willmer and Wright (1945) from the colour mixture curves for the human fovea, when viewing objects at small visual angles, it was found to have two crests—one at about 5,600 A.U. and the other at about 6,000 A.U. (Fig. 2). Further, in persons with green deficiency the crests of the red response curves differ in position, and in subjects with defective green vision they also vary (Figs. 3 and 4). When the troughs of the red response curves are similarly considered it is found that they also differ in position in the spectrum according to their derivation. Thus the curve obtained from colour mixture measurements has a trough at 5,000 A.U. (Fig. 1). That for reduced foveal colour vision has one at 4,600 A.U. (Fig. 2); while green-blind persons (deuteranopes) have a red response curve that has a trough at 4,400 A.U. (Fig. 3).

The green response curve is not so variable in shape as the red, but in this case also some differences occur which are hard to explain. The blue response curve has a crest which varies from about 4,500 to 4,800 A.U., but this may be caused by individual peculiarities in macular pigmentation.

Section V: Hue Discrimination

When a person with normal colour-vision looks at a spectrum there are parts where there is a rapid change of hue, and other parts in between where the change is slow. Thus it is particularly slow at the extreme red and violet ends of the spectrum and particularly rapid in the yellow. A thorough examination of the spectrum shows that there are four places where discrimination is good, which separate five places where it is poor (Fig. 5). Now the three-colour theory can account for only two of the good points and for only three of the poor ones (Fig. 6). This is so because good discrimination depends on the overlapping of the sensations, so that one—for example, the red—is diminishing at the same time that its neighbour, the green, is increasing, with change of position in the spectrum. Since

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FIG. 10

FIG. 11

Figs. 1, 2, 3, 4, 10, and 11.—Wave-lengths horizontal; intensity in arbitrary units, vertical.

Figs. 5, 6, 7, 8, and 9.—Wave-lengths horizontal; colour discrimination in arbitrary units, vertical.

FIG. 1.—Red response curve for a subject with normal colour vision. FIG. 2.—Red response curve for reduced foveal colour vision. FIG. 3.—Red response curve for a green-blind (deuteranopic) subject. FIG. 4.—Red response curve for a green-defective (deuteranomalous) subject. FIG. 5.—Hue discrimination curve for a subject with normal colour vision. FIG. 6.—Normal hue discrimination curve calculated by Helmholtz, from Young's theory. FIG. 7.—Hue discrimination curves: A, for a red-blind (protanopic) subject; B, for a green-blind (deuteranopic) subject. FIGS. 8 and 9.—Hue discrimination curves for reduced foveal colour vision. FIG. 10.—Luminosity curves: A, for a red-blind (protanopic) subject; B, for a green-blind (deuteranopic) subject. FIG. 11.—Luminosity curve for reduced foveal colour vision.

there are two such places of overlap, one between the red and green and the other between the green and blue, two regions of good hue discrimination can be accounted for. This was found by calculation, both by Helmholtz and by Judd (Fig. 6). These ideas are substantiated by an examination of the hue-discrimination curves either of red-blind or of green-blind subjects, for in both cases the curves are U-shaped (Fig. 7), the centre of the trough occurring at the point of the spectrum where the response curves are undergoing the greatest relative change for a given alteration of wave-length. On the contrary, at parts of the spectrum where there is only one response curve present, there is no hue discrimination at all, and the curve in consequence shoots up to very high values. It does this on both sides of the trough, thus causing the curve to have a U shape. Now according to Young's theory of the three fundamental receptor processes, if one type is missing only two remain; thus both red-blind and green-blind persons are called "dichromats." Dichromatism is consequently always associated with a U-shaped hue-discrimination curve. Subjects with trichromatic vision would therefore be expected to have a double U-shaped curve, as both Helmholtz and Judd (1932) calculated to be the case.

How, then, can a curve be accounted for, consisting of four U's, such as persons with normal vision are found experimentally to possess? It would seem evident that their colour-vision must be mediated by not less than five types of receptor. Some further evidence on this point will be given in the next section.

Section VI: Vision of Objects Subtending Small Angles at the Eye

There are several conditions which cause a subject with normal colour-vision to become temporarily colour-deficient or even colour-blind. Three of these conditions will be discussed here—namely, (1) a reduction of visual angle; (2) a reduction of illumination; and (3) the use of peripheral vision. Under all these conditions, with suitable adjustment, colour-vision gradually becomes defective,

until finally a state of total colour-blindness is attained. In all three cases there appears to be a clearly marked intermediate stage between full colour-vision and complete colour-blindness, at which the subject is partially colour-defective. For this intermediate type of vision I have suggested the name "reduced colour-vision." From what has been stated above it may be inferred that there are three types of this: type 1, that produced by a reduction of visual angle; type 2, that produced by a reduction of light intensity; and type 3, that produced by the employment of the periphery of the retina. The first two types appear to have much in common; in fact, it may be found that they are identical in their properties. The third type is entirely different from the other two (see Section VII).

Type 1.—When coloured objects which subtend very small angles at the eye are looked at their colours become altered. Blue is replaced by dark grey or black, and yellow by pale grey or white. Other colours are also seen to change. Thus green loses its yellow tint and is replaced by blue-green; crimson is replaced by orange; and purple and mauve alter to shades of brown. Four colours seem to undergo hardly any change at this stage—red, orange, blue-green, and greenish blue. White undergoes no perceptible change at all. According to Willmer (1944), and to Thomson and Wright (1947), this change in

colour-vision is due to a temporary defect in the blue receptors, as if the retina had become locally blue-blind. If this were the case, then on the three-colour theory two sensations would be left in action—namely, the red and the green. Therefore white, since it stimulates both sensations, should look yellow, and so the colours seen by the eye should be red, yellow, green, and various hues made by their mixture. But the colours seen are red, orange, white, blue-green, and greenish blue, so that the explanation offered by Willmer and by Thomson and Wright seems to be at variance with the facts. A further piece of evidence against the acceptance of their explanation is the fact that a decrease in the brightness of the spectrum occurs both in the yellow and in the blue when normal colour-vision is replaced by reduced colour-vision, as is shown by the change in the shape of the luminosity curve obtained by Wright (1943) (see Figs. 10 and 11). Now, a decrease in the blue would be expected on their hypothesis, but not a decrease in the yellow as well; so that in this respect also their hypothesis does not seem to fit the observed facts. But there is a further difficulty in accepting their conclusion—namely, that if reduced colour-vision is equivalent to tritanopia, caused by the temporary insensitiveness of the blue receptors, then according to Young's theory a form of dichromatism should remain, and thus the hue-discrimination curve should be of the simple U type as shown in Fig. 7. Thomson and Wright (1947) did not obtain such a curve, however, but curves with a more complex form as shown in Figs. 8 and 9. This indicates the presence of a more elaborate type of vision than that provided by two receptors only. In my view reduced foveal vision is mediated by at least four receptors: red, orange, blue-green, and greenish blue; then the addition of yellow and blue in order to reconstitute full colour-vision should involve six types of receptor at least. Such a supposition is completely at variance with the trichromatic theory.

Type 2.—The reduced colour-vision which is found under conditions of feeble illumination was investigated by Abney and Festing (1892). They found that at an illumination of 0.0025 f.c. the spectrum appeared to begin at 6,250 A.U. in the orange, and reached its full intensity at 6,000 A.U. From there the colour became progressively paler, with change of wave-length, until all colour was lost at about 5,800 A.U. in the yellow. The spectrum remained colourless to 5,650 A.U., where a blue-green tint slowly developed, to reach its maximum at 5,200 A.U. This darkened and ceased to have a noticeable colour at about 5,000 A.U. in the blue-green part of the spectrum. Thus the red and blue ends of the spectrum had been replaced by dark grey or black, and yellow had been replaced by pale grey or white, as is found to be the case with the reduced colour-vision (type 1) caused by a reduction of visual angle. I have found that for every light intensity from 3,000 to 0.01 f.c. there is a corresponding visual angle at which full colour-vision is replaced by reduced colour-vision.

Type 3 will be considered in the following section.

Section VII: The Colour-vision of the Periphery of the Human Retina

If coloured test objects be examined first by the fovea centralis and then by a more peripheral part of the retina it will be found that certain of them undergo changes of colour or brightness. The colour-changes are summarized in the Table, together with those for reduced foveal colour-vision produced by a decrease in visual angle, which were considered in the previous section.

Table showing Colours Seen by Peripheral and by Reduced Foveal Vision

Colour	Periphery	Reduced Visual Angle
Red	Dark yellow-brown	Red
Orange	Yellow-brown	Orange
Yellow	Yellow	Pale grey
Green	Yellowish grey	Pale blue-green
Blue-green	Grey	Blue-green
Violet	Dark blue	Black
Purple	Dark blue-grey	Dark red-brown
Mauve	Dark yellow-brown	Red-brown
Crimson	Yellow-brown	Orange
White	White	White

These changes may be contrasted as follows: with a reduction of visual angle the yellow and the blue drop out, leaving red-orange and blue-green; with peripheral vision, on the contrary, it is the red-orange and the blue-green which drop out and yellow and blue which remain. Thus they appear to be the antithesis of one another. During both changes it should be noticed that white continues to be seen as white, indicating, in my opinion, that in both cases the colours which fall out are complementary pairs, leaving complementary pairs behind. Thus if the retina contained three pairs of complementary receptors—red and its complementary blue-green, orange and its complementary greenish-blue, and yellow and its complementary blue—and if these dropped out in pairs it would fit in with several of the observed facts. This does not exclude the possibility that, in addition to the complementary pairs just mentioned, there are other receptors which function in normal vision.

Section VIII: The Rival Theories

Only when the colour properties of peripheral vision remained apparently unaccounted for by Young's theory was there the possibility that one day the problem would be satisfactorily cleared up. But now that this theory is out of line with modern work on foveal vision, hue discrimination, micro-stimulation, micro-electrode results, and even colour-mixture and colour-blindness, the confidence of even its strongest supporters is shaken, and they give consideration to other theories of colour-vision.

Colour-mixture and micro-stimulation both suggest seven receptors; hue discrimination, more than five; reduced foveal vision, six or more. So that some form of polychromatic theory would seem to be indicated. If that proves to be the case a question that will arise is this: Why has vision been thought to be trichromatic for so long—in fact, until the recent introduction of more critical methods of research? One possible explanation may be founded on Granit's observations on frogs, for he discovered three main groups of receptors—a red group with crests at 6,000 and 5,800 A.U., a green group with crests at 5,400, 5,200, and 5,000 A.U., and a blue group with crests at 4,600 and 4,400 A.U. Now, it is possible that these act in group formation not because their nerve fibres are interconnected to form three main sensations but because of the overlapping of their response curves. Thus one touch-spot may behave as a single unit neither because it contains only one touch-sense organ nor because the nerve fibres of all the touch-sense organs present are interconnected, but because a force applied to the skin almost always stimulates them at the same time.

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Wiltshire has now adopted a scheme for part-time nursing similar to that working successfully in Gloucestershire, and it is hoped to recruit volunteers particularly from outlying districts by the provision of adequate transport to and from work.