Recent Advances in Color Vision

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MANY THEORIES OF COLOR VISION have been suggested from time to time. Most of them have received little support, but two have been exceptions in this respect, namely, Young's three-color theory and Hering's four-color theory. The former is in apparent conformity with color mixture and with color deficiency data, while the latter is superficially in agreement with other important aspects of human color vision. The polychromatic theory to be dealt with in this address is the outcome of an attempt to combine together the good features of both of these older theories.

According to Young's theory human color vision is provided by a tricolor unit. On the other hand, according to Hering's theory it is provided by two units: a yellow-blue unit and a red-bluegreen-red unit. The polychromatic theory proposed by the author adopts the tricolor unit as its principal agent and the yellow-blue and red-bluegreen-red units as its subsidiary agents. Thus, human color vision is nearly trichromatic but not quite, because in addition to the tricolor unit there are also present the two additional units just mentioned.

Here, then, is an outline of the polychromatic theory.

Polychromatic theories have been advanced by Wundt, by Edridge-Green, and in a modified form by Shaxby. Granit's modulators also form, in some animals, what amount to a polychromatic series. The polychromatic theory advanced by the author differs from all these in important respects, and it is not proposed to deal further with them here, but instead to describe briefly the circumstances which lead to the development of this particular theory.

Until a few years ago experimental work appeared to support unequivocally the three-color theory of Thomas Young. When the author first observed the change of yellow to pale gray or white, and of blue to dark gray or black, which play so essential a part in the antichromatic responses, he endeavored, apparently with success, to account for them on this classic theory. But further facts then came to light incompatible with that theory. These facts were: (1) the change in the shape of the luminosity curve with reduction of light intensity, and the development of a notch (*26*); (2) the corresponding change in the shape of the luminosity curve with reduction of visual angle (*33*); (3) the finding by the author (*9*) of more fixation points in the fovea than three; (4) the finding by the author of more specific colors than three, as the result of applying microstimulation to the retina in the presence of suitable conditioning stimuli. These results, incompatible with the three-color theory, led to a re-examination of the whole subject of color perception.

The outcome of that survey convinced the author that, under average conditions of lighting, adaptation and field size, the three-color theory is a useful approximation so far as foveal vision is concerned. It is the truth but not the whole truth, because it is not in accord with a large mass of evidence, much of which has been obtained recently, partly by using improvements on older methods, such as the mixture of spectral colors by means of the Wright spectroscope, and partly by the development of entirely new methods—for example, the Stiles and Crawford (*30*) technique. But much older work was also found at variance with the three-color theory. When all this evidence has been taken into account, it would not be unfair to sum up by stating that there is hardly a single phase of human color vision which does not support a polychromatic theory more strongly than it does one based only on three colors.

I. THE POLYCHROMATIC THEORY

The polychromatic theory postulates the existence of two subsidiary visual units in addition to the tricolor unit of Young's theory. One of these, the Y-B unit, has receptors with response curves having crests in the yellow and in the blue parts of the spectrum. The other unit, the R-BG-R unit, also comprises two types of receptors, and these have response curves with crests in the red and in the blue-green part of the spectrum, but the former have, in addition, secondary curves in the extreme violet part of the spectrum. This fact is indicated by the duplication of R in the title of the unit.

When the fovea is being used in normal color vision, all three units are in action. When a more peripheral part of the retina is in use, the Y-B unit alone provides color vision. The fovea at very high light intensities also employs this unit alone, whereas at low intensities

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or small visual angles the R-BG-R unit functions alone. With white stimuli, all the constituent receptors of the functioning units receive adequate stimulation. When, on the other hand, the objects under examination are colored, the receptors which are stimulated are those which have response curves in the corresponding part or parts of the spectrum and which belong to functioning units. The following example may make this clearer: Suppose the ray incident on the retina to be red of 0.65 μ; then the stimulated receptors are the long wave-length receptor of the tricolor unit, the red receptor of the R-BG-R unit and the yellow receptor of the Y-B unit. If the ray which falls on the fovea is of medium light intensity, all three units will be potentially in action, and the sensation aroused by their combined actions will be a somewhat orange red.

At very high intensities, however, as stated above, the only active unit is the Y-B one, and in consequence the sensation aroused by the stimulus of wave-length 0.65 μ will be yellow. At low intensities the only active unit is the R-BG-R one, and the sensation aroused will consequently be a purplish crimson, since this is the hue produced by the activity of the red receptor of this unit which, as stated above, has response curves in both the red and the violet parts of the spectrum. These theoretical conclusions agree with experiment.

TABLE 1

Visual unit	Position of receptor in the spectrum	Probable wave length of crest of response curve*
Tricolor	Orange	0.610
"	Green	0.545
"	Indigo	0.450
Y-B	Yellow	0.575
"	Blue	0.473
R-BG-R	Red and violet	0.670 0.360
"	Blue-green	0.495

* These wave lengths are approximate only.

These three units together comprise 7 different types of receptor, and these have 8 response curves, the spectral positions of which are indicated in Table 1.

When white light falls on the retina, it stimulates all receptors of active units. Thus, at the fovea under medium light intensities all 7 receptors will be active, at high intensities the yellow and the blue receptors only, at low intensities the red and the blue-green receptors only. At the dichromatic zone of the periphery of the retina the yellow and the blue receptors are those which are stimulated, because the Y-B unit is the only one which is potentially active. This accounts for the large sizes of the yellow or blue fields in comparison with those of red and green. It is clear, therefore, that according to the present polychromatic theory all 7 types of receptor are in use only at medium light intensities at the fovea and the parafovea. At other intensities and in the periphery of the retina a simpler receptor arrangement is in use. As the visual angle is reduced, first the Y-B unit becomes inactive, then the tricolor unit, finally leaving the R-BG-R unit alone in action. The author has produced evidence that these changes are not limited to the foveal center but take place in all parts of the retina where all three units are normally in action.

II. HUE DISCRIMINATION

It will be remembered that there are two classes of subjects who are able to pass successfully the ordinary tests for color blindness—the normal trichromats and the anomalous trichromats. The latter are subdivided into two classes according as they require more red or more green than the normal sighted, in order that a red-green mixture shall match a given yellow. Those who require more red and are therefore somewhat red blind are called protanomalous, since they approximate the completely red blind or protanopic. Those who require more green and are therefore somewhat green blind are called deuteranomalous, since they approximate the deuteranopic subject.

There are two varieties of protanomalous trichromat —a primitive type and a more advanced type. The hue discrimination curve of the former consists of two U-shaped parts having troughs at about 0.49 and 0.59 μ. To account for this curve three types of receptor are required, namely, in the long, medium, and short wave region of the spectrum. The hue discrimination curve of the better type of protanomalous subject, such as Wright's observer A, shows improvement in the green part of the spectrum. To account for this improvement, an additional receptor is required, probably in the blue-green part of the spectrum. Investigation shows that an alteration of position, or a change of width, of the response curve of one of the three receptors mentioned above does not bring about the improvement shown on comparing the curves.

The color vision of the normal subject as found by Pitt and Wright (1934) shows improvement at about 0.44 μ over that possessed by observer A, and there is a second region of improvement near the orange part of the spectrum. To account for these improvements, two additional types of receptors are required, in the blue and the yellow. Finally, some normal-sighted observers, such as Steindler (*27*), Jones (*16*), and Laurens and Hamilton (*20*), appear to have better hue discrimination still, particularly in the red part of the spectrum. This calls for an additional type of receptor.

Calculations of the hue discrimination curve of normal-sighted subjects have been made by Helmholtz (*11*), Judd (*17*), Stiles (*29*), and others, on the basis of the three-color theory. These calculated curves are far from being identical in shape with the experimental curves obtained with normal-sighted, protanomalous (including Wright's observer A), and deuteranomalous observers, as should be the case because, according to the three-color theory, all these three classes are 'trichromats.' Thus, the three-color theory fails to give a satisfactory account of the hue discrimination of these subjects. The polychromatic theory, on the other hand, postulates 3 types of receptor for the more primitive protanomalous subject, 4 types for the more advanced type, probably 5 types for the deuteranomalous, and 7 types for subjects with normal color vision.

III. Tristimulus Spectral Mixture

It is well-known that when the different parts of the spectrum are matched using as stimuli a red of 0.65 μ, a green of 0.53 μ, and a blue of 0.46 μ, trichromats usually find that most of the spectral colors are more saturated than the mixtures. These differences of saturation are noticeable in four main spectral regions: in the red near the long wave end of the spectrum, in the yellow, in the blue-green, and in the violet near the short wave end of the spectrum.

Trichromats differ markedly from one another in their ability to match the rays corresponding to these spectral regions with the three matching stimuli. These differences, so far as the yellow and blue-green are concerned, are summarized in Table 2.

In Table 2 the various classes of trichromat are arranged in order, the more primitive protanomalous subject first, because the differences in saturation of the monochromatic spectral colors and the mixed colors are very small, or absent. Then comes the improved kind of protanomalous subject such as Wright's observer A; then the fovea of the normal-sighted subject; then the parafovea of the normal-sighted subject; and lastly, the deuteranomalous subject to whom the blue-green spectral colors are far more saturated than the mixture of the green 0.53 μ and the blue 0.46 μ.

The differences in saturation between the monochromatic and the mixed colors are accounted for on the three-color theory by supposing that the three-receptor processes have poor spectral selectivity—that is, that their response curves spread over much of the spectrum. Thus, the blue response mechanism is sensitive to almost all greenish rays as well as to blue ones; the green response mechanism is sensitive to almost all rays; and the red response mechanism is sensitive to almost all green rays, as well as to yellow, orange, and red ones. In consequence, monochromatic yellow light, which acts as a stimulus to both the red and the green response mechanisms, but not to the blue ones, appears, according to this hypothesis, to be more saturated than a red and green mixture which stimulates not only the red and the green mechanisms but the blue ones as well.

In support of this hypothesis MacAdam (*22*) has pointed out that, when reproduced by a three-color photographic process, spectral yellow is more saturated than a red-green mixture. In this case there can be no doubt that the wide overlap of the response curves of the three color-selecting filters is responsible for the observed differences of saturation.

Suppose that this argument be accepted in the case of human color vision. It is then found to lead to the conclusion that subjects who do not find differences of saturation between monochromatic and mixed colors—that is, subjects who are protanomalous trichromats—either have receptors of narrower response (*i.e.* of greater selectivity) than other trichromats, or that their saturation discrimination is poor, so that they make matches which would be unacceptable to normal subjects who are better in this respect. Now Chapanis (*4*) has shown that the latter is not true, because, so far as the yellow region of the spectrum is concerned, the protanomalous possess better saturation discrimination than the normal-sighted do. It is therefore concluded that their receptors have better selectivity because the response curves of these receptors do not overlap as much as they do in the normal sighted. On comparing similarly protanomalous with deuteranomalous trichromats it is concluded that the former have receptors with much greater selectivity than those of the latter. Now receptor selectivity plays a fundamental part in color vision because poor selectivity must cause all colors to look much alike, so that no color approaches in saturation that which would be produced by the stimulation of a single type

TABLE 2

Type of subject	Negative coefficients	
	Red stimulus in blue-green part of spectrum	Blue stimulus in yellow part of spectrum
Normal protanomalous	Nil	Nil
Improved protanomalous	2–3%	Nil
Normal fovea	10–12%	3–5%
" parafovea	10–12%	10–12%
Deuteranomalous	Over 12%	Under 3%

of receptor only. Vice versa, high receptor selectivity must cause colors to appear to possess a high degree of saturation. On these grounds, of all the types of subject with trichromatic vision mentioned in Table 2, the protanomalous must have the best color vision and the deuteranomalous the worst.* The normal-sighted come in between, with the fovea superior to the parafovea. Now these conclusions are completely at variance with the facts, for the protanomalous are little better or worse than the deuteranomalous, and both are greatly inferior to the normal-sighted, in whom the parafovea is superior to the fovea.

According to the polychromatic theory the monochromatic colors have superior saturation to the mixed colors because the former stimulate an additional receptor more strongly than do the latter. Thus, to the normal-sighted subject spectral yellow is more saturated than a red-green mixture, because the former stimulates yellow receptors strongly and red ones and green ones feebly. On the contrary, the red-green mixture stimulates the red and green receptors strongly but the yellow ones feebly. In a similar manner enhanced saturation of the monochromatic spectral colors in the extreme red is caused by the additional type of receptor which operates in this part of the spectrum. Additional blue-green receptors improve saturation in the blue-green region, and additional violet receptors in like manner improve short-wave saturation. Since, to the primitive type of protanomalous subject, the single spectral colors and the spectral mixtures which match them are alike in saturation, no additional receptors are present, and their color vision is mediated by the fundamental tricolor unit alone. Thus, of all so-called trichromats, they should have the most inferior color perception. The improved type of protanomalous subject, to whom the blue-green rays are more saturated than are blue and green mixtures, has the additional blue-green type of receptor according to the polychromatic theory, and therefore is superior to the more primitive protanomalous subject in this respect. The position of the deuteranomalous subject is not entirely clear, but according to present evidence he possesses both the tricolor unit and the blue-green and possibly also the red receptors of the R-BG-R unit. But the former is outweighed by the latter so that he approximates a dichromat, and this accounts for his inferior color vision. For normal foveal vision 7 types of receptor are required, the three-color unit and the four additional receptors of the Y-B and the R-BG-R unit, the former strongly and the two latter, particularly the Y-B unit, feebly. At the parafovea, so far as present evidence goes, the same 7 types of receptor are present, but the additional ones hold a more prominent position, so that they play more nearly the same part as that played by the tricolor unit.

According to the polychromatic theory, therefore, both the protanomalous and the deuteranomalous have inferior color vision to the normal-sighted subject; in the latter, the parafovea has superior color vision to the fovea, and these deductions are found to be in harmony with the results of experiment.

IV. THE RETINAL DIRECTION EFFECT

When a narrow pencil of monochromatic light traversed the pupil horizontally, Stiles (*28*) found changes in brightness, hue, and saturation. The author (*9*) has pointed out that the magnitude of the brightness effect for yellow rays is substantially less than it is for either red or green rays. This makes it unlikely that yellow rays stimulate red and green receptors alone, as is postulated by the three-color theory. It is more probable that there are specific yellow receptors having a different intensity direction effect from that of the red or green receptors. The other aspects of the retinal effects on intensity can be accounted for on the three-color theory.

Stiles (*28*) found that the variations of hue with wave length are more complex than would be expected on the three-color theory. On this theory there are only 8 possible combinations, of which the two exhibiting the greatest variation with wave length are red +, green –, blue +, or vice versa: red –, green +, and blue – (that a single crest in the green with lower values in the red and in the blue, or a single trough in the green with higher values in the red and the blue). Now Stiles obtained on the temporal side of the pupil a graph exhibiting two troughs and one crest, whereas on the nasal side the graph showed more detailed changes still, namely, two troughs and two crests. In order to account for the former a minimum of four types of receptor are required; in order to account for the latter a minimum of five types. Unfortunately, Stiles has not investigated the phenomenon with sufficient detail for a more precise estimate to be made of the number of types of receptor required, but there would seem to be no difficulty in doing this.

With regard to the third retinal direction effect, namely, on saturation, Stiles has not given any details of this beyond mentioning the fact that such variations exist. No statement is possible at the moment, therefore, as to its value in the elucidation of the problems of color vision. The effects on brightness and hue may be summarized as follows: the brightness effect requires at least four receptors, of which yellow must be one; the hue effect requires at least five.

Further study of the effects may show the necessity for more.

V. PERIPHERAL VISION AND REDUCED FOVEAL VISION

The term 'reduced foveal vision' has been used by the author (*9*) to denote the type of hue perception found at the fovea at low light intensities and at small visual angles. Reduction of intensity or visual angles results in the replacement of full color vision, first by a form of dichromatism and then by colorless foveal vision. In the dichromatic stage, colors are seen in terms of two primaries only, red and blue-green, and mixtures of these with white, gray, or black. The author attempted to account for this type of vision on Young's theory by supposing a type of linkage to occur between the green and the blue receptor pathways, but this supposition had to be abandoned when the changes in the shapes of the luminosity curves found by Sloan (*26*) and Willmer and Wright (*33*) were taken into account. During the changes just referred to, many colors, both spectral and mixed, undergo alterations in hue, but there are four invariable colors: blue, blue-green, yellow, and red. The blue and the yellow are replaced by colorless shades of gray at an early stage of the change; the blue-green and red are similarly replaced by grays, but at one of the last stages.

When foveal vision is gradually replaced by peripheral vision, color perception becomes reduced until, as in the case of foveal vision, a colorless state is obtained. At an intermediate stage in this change dichromatic vision occurs in which colors are seen in terms of yellow and blue and mixtures of these with white, gray, or black. In this case, also, four invariable colors are found (blue, blue-green, yellow, and red), but whereas with reduced foveal vision the yellow and the blue suffer early replacement and the blue-green and the red suffer later replacement by grays, in this case of peripheral vision the situation is reversed. Attempts have been made to account for these changes in color vision on Young's theory, by supposing that linking occurs between the red and the green receptor pathways. Thus, the vision of the blue-yellow zone of the periphery is identified with the dichromatic vision of the deuteranopic subject in whom permanent linkage of these pathways is supposed to be present. But this supposition also is rendered untenable by an examination of the liminosity curves, because that of the dichromatic zone of the retinal periphery was discovered to have a crest at 0.59–0.60 μ (*19*). When these values were corrected for an equal energy spectrum by the author, the crest of the luminosity curve shifted to a wave length of about 0.58–0.59 μ. Now the crest of the luminosity curve of the deuteranope, as found by Pitt (*23*), occurs at 0.56 μ. Thus, the suggestion of linking between certain receptor pathways has to be abandoned. These difficulties introduced by the liminosity curves are not the only ones making the position of the three-color theory untenable.

According to the polychromatic theory, with reduction of visual angle or lowering of light intensity, or both, the Y-B-unit is the first to become inactive, and this is followed by the tricolor unit. In consequence, the R-BG-R unit is the only one in a state of activity. The notches in the luminosity curve observed by Sloan (*26*) and by Willmer and Wright (*33*) are due to the inactivity of the Y-B unit in the blue and in the yellow parts of the spectrum. On the other hand, when a more peripheral part of the retina is employed, the first unit to become inactive is the R-BG-R, and this is followed by the tricolor unit. At this stage the only unit in action is the Y-B one, and this has the luminosity curve found by von Kries.

So far no mention has been made of the effects of increasing light intensity. The color changes as found by Purdy (*24*) strongly resemble those produced by using a peripheral part of the retina. If the illumination be sufficiently bright, there is colorless foveal vision; at a less intense illumination there is yellow-blue vision, which, according to the polychromatic theory, is due to the activity of the Y-B unit. Thus, the polychromatic theory accounts for these phases of color vision by postulating activity of certain visual units and the inactivity of others, and in this way accounts for their properties in a satisfactory manner.

VI. THE CONSTANCY OF WHITE

When identical pairs of colored test objects are examined, one by the fovea and the other by the periphery of the same eye, most of them are found to differ; yet when white test objects are similarly examined, no differences can be detected. When similar experiments are performed to test the effects of light intensity or of size of visual angle, colored test objects are found to undergo marked differences, but white test objects similarly tested are found to undergo no observable change. This constancy of white is the more remarkable because deviations from white are so readily noticed.

Now according to the three-color theory, the perception of white is due to the stimulation in a certain fixed ratio of all three receptor processes, so that the constancy of white proves that this ratio is the same for the periphery of the retina as it is for the fovea and is the same at the fovea for high light intensities as for low ones and for large visual angles as for small ones. The important color changes which are found to occur under these different conditions make it imperative that there should be alterations in color perception, and yet the constancy of white shows that they cannot occur so far as the three-color theory is concerned.

While great difficulty is experienced on the three-color theory, no such difficulty faces the polychromatic theory, because it is the property of the three units, either separately or in combination, to respond to a white stimulus by means of a white sensation. Suppose, for sake of argument, that orange, green, indigo, and purple be examined (a) by the dichromatic zone of the retinal periphery where the Y-B unit is found in a pure state and (b) by the dichromatic vision of the fovea at a small visual angle which is mediated by the R-BG-R unit; then these colors will all be found to exhibit marked differences when examined first by the one type of vision and then by the other. But white similarly tested will be found to undergo no change, because, as stated above, both the Y-B and the R-BG-R units respond to a white light stimulus with a white sensation.

VII. THE EFFECTS OF LIGHT INTENSITY, ADAPTATION, AND VISUAL ANGLE ON FOVEAL SPECTRAL MIXTURE

Various factors have been found to affect the matches between monochromatic spectral colors and mixtures of spectral colors. Thus, von Kries (*18*) investigated the effects of light intensity; Wright, the effects of adaptation (*34*); and Hering (*12*), Horner and Purslow (*14*), and Shaxby (*25*), the effects of visual angle on the match between yellow and a red-green mixture. These effects, recently confirmed by the author, are summarized in Table 3.

TABLE 3

	Red-green mixture compared to pure yellow
High intensity	Greener
Low "	Redder
Light adaptation	Greener
Dark "	Redder
Large visual angle	Greener
Small " "	Redder

The three-color theory, which postulates that yellow and a red-green mixture resemble one another in stimulating the red and the green receptors, finds it difficult, if not impossible, to account for these disturbances of color matches. Attempts to account for them on the grounds of the selective absorption of the yellow pigment of the fovea or of the greater "rod value" of green are both found to fail. According to the polychromatic theory, on the other hand, there are independent receptors for red as well as for orange, for yellow, and for green. The red ones, since they belong to the R-BG-R unit, play a more important part in foveal vision at low light intensities, at small visual angles, and when adapted to low light intensities. Thus, under these conditions the red component of the red-green mixture is accentuated, and this disturbs the match with yellow.

VIII. SELECTIVE ADAPTATION

Burch (*2, 3*) concluded from fatigue experiments that the human retina contains four types of receptor: red, green, blue, and violet. He was unable to obtain evidence for a fifth type of receptor, namely for yellow rays.

Allen (*1*), after fatiguin[illegible] [illegible]ys of 0.589 µ or of 0.577 µ, found that th[illegible] noticeably reduced both in the red and in the green but hardly at all between 0.64 µ and 0.58 µ. This was held to be evidence that yellow rays are perceived owing to the stimulation of red and green receptors but not of specific yellow receptors.

Edridge-Green and Marshall (*5*), after exposing the eye for a short time to a sodium lamp, claimed that they found unmistakable evidence for separate yellow receptors. The author (*10*), using yellow color filters, both monochromatic and dichromatic (red and green), of sharp spectral cut-off and equal visual appearance, found on fatiguing the eye that different results were obtained. After fatigue with the monochromatic yellow light the spectrum appeared to be greatly modified in appearance: yellow appeared neutral gray, red and orange appeared crimson, yellow-green and green appeared blue-green, and blue and violet were much darkened. On the other hand, exposure of the eye to the red and green mixture darkened the entire spectrum and produced slight selective effects on the colors of its different parts, but not of the same degree as those produced by the monochromatic yellow light. On the trichromatic theory it is difficult to explain why these two lights which resemble one another so closely should produce different fatigue effects. According to the polychromatic theory, on the contrary, the monochromatic yellow light stimulates the yellow receptors strongly and the orange, red, green, and blue-green receptors feebly. The dichromatic yellow light stimulates the red, orange, green, and blue-green receptors strongly and the yellow receptors feebly; hence, different results are achieved on subsequently examining a spectrum.

It remains briefly to refer to the curious inhibiting effect which exposure of the eye to monochromatic yellow light has on the subsequent perception of blue and violet, and that which exposure of the eye to blue or violet has on the subsequent perception of yellow. This is paralleled by similar effects when both are situated side by side in the same visual field, attention to which has been directed previously by the author (*9*). It would appear possible that both simultaneous and subsequent presentation operate in a similar manner just as simultaneous and successive contrast appear to do. It is hoped to deal elsewhere with this subject in greater detail.

IX. SATURATION DISCRIMINATION

The apparent saturation of the spectral colors is disturbed by actual or potential neutral points caused by the response curves of the receptors occupying complementary or nearly complementary positions in the spectrum. Thus, for the protanope who possesses two types of receptor only, which are complementary to one another, there is an actual neutral point at about 0.49 μ.

Let us take a second example. To the fovea of the normal subject when observing test objects at small visual angles, there is dichromatic vision probably due to the activity of the R-BG-R unit in a pure state. Now the red and blue-green receptors are complementary to one another, and in consequence there are two actual neutral points, at 0.578 μ and 0.41 μ (*33*).

Let us now take a third example. It was found by Chapanis (*4*) that to the protanomalous subject the spectrum at 0.49 μ is nearly neutral and there is a second, not well-marked, potential neutral point at 0.56 μ. In these subjects, who have only three types of receptor in a functional state, no one pair is complementary to any other pair, but the red and green receptors produce the potential neutral point at 0.56 μ and the two acting together produce with the blue receptors the nearly neutral point at 0.49 μ. Now the tricolor unit of the normal-sighted subject closely resembles, if it is not identical with, the visual unit of the protanomalous subject. If this be correct, the tricolor unit is responsible for one nearly neutral point at 0.49 μ and for one point of poor saturation at 0.56 μ. Similarly, the Y-B units of the normal-sighted is found to have an actual neutral point at 0.526 μ, and, as we have seen, the R-BG-R unit possesses two actual neutral points at 0.578 μ and at 0.41 μ.

Taking these neutral points in turn, there are two in the yellow, one caused by the R-BG-R unit and one by the tricolor unit. These correspond in wave-length to the crests of the yellow receptors of the Y-B unit. Now this is only a subsidiary unit, so that the yellow receptors modify but slightly the potential neutral point produced by the other two units. The consequence is that the yellow region of the spectrum is a point of low saturation. The next neutral point in the spectrum is at 0.526 μ, due to the Y-B unit, but this is close to the crest of the important green receptors of the tricolor unit, the consequence being that this potential neutral point does not disclose its presence in normal color vision. In a similar manner the neutral point at 0.49 μ due to the tricolor unit coincides almost exactly with the crests of the blue-green receptors of the R-BG-R unit and is thus covered up. Lastly, the neutral point at 0.41 μ belonging to the R-BG-R unit is not far removed from the crests of the indigo receptors of the tricolor unit and is thus hidden by them. The conclusion is that of all these potential neutral points, the only one of consequence in normal vision is the one which occurs in the yellow part of the spectrum. This conclusion, which has been arrived at on the basis of the polychromatic theory, is in good agreement with the experimental data, because, as is well known, the point of lowest saturation in the spectrum is in the yellow. The three-color theory can offer no explanation of the variation of saturation with wave length exhibited by the protanomalous and the normal-sighted.

X. THE ANTICHROMATIC RESPONSES, THE FIXATION POINTS, AND THE SUBJECTIVE COLORS

Having reviewed in the previous sections some of aspects of human color vision for which the three-color theory is unable to provide a satisfactory account, but which can be explained on the polychromatic theory, it is now necessary to re-examine the experiments referred to in the introduction, which, being of a subjective nature, might not alone be considered to carry much weight, but materially add to the evidence given in the foregoing sections. The experiments referred to are those on the antichromatic responses, the separate fixation points of the different colors, and lastly, the subjective estimates of hue when, by means of a microstimulator and in the presence of conditioning stimuli, a tenuous beam of white light is caused to explore the retina.

Ever since the days of Thomas Young it has been agreed that the lens system of the eye suffers from chromatic aberration. The most recent measurements of the aberration at different wave lengths were made by Ivanoff (*15*) and by the author (*9*). Agreement between them is extremely good—so good, in fact, that further estimates on healthy emmotropic or nearly emmotropic subjects would appear to be unnecessary.

Now an examination by means of a microscope or high-power eyepiece of the images produced by uncolor-corrected lenses shows that color fringes are present at the borders separating the light and dark parts of the pattern present in the visual field. These fringes at the optimum focusing point are yellow and blue. But it is a matter of everyday experience that their presence is seldom observed in normal vision. Experiments of a simple and reliable nature using blue and yellow test objects, those produced both by the use of dyes and color filters and by means of a suitable spectrometer, show that there is present in connection with vision a mechanism of some kind which can eliminate not only the colored fringes produced by the chromatic aberration of the eye but the colors of yellow and blue test objects as well. Experiment shows that many factors are concerned with this elimination—the intensity of illumination, the relative intensities of the spectral components present in the fringes, etc. Of special importance is the proximity of yellow and blue, because this is found to facilitate greatly the loss of hue by both colors. A number of different hypotheses have been advanced by the author to account for these facts, but one alone stands up to detailed examination, one, moreover, which is based on the polychromatic theory, namely, that the proximity of the blue and the yellow fringes, which is always found to occur when they are produced by chromatic aberration, aids the inactivity in the first place of the Y-B unit and in the second place of the tricolor unit, so that the only visual unit left in action is the R-BG-R unit. There is evidence supporting the view that these changes are brought about by a nervous mechanism which has been called by the author the antichromatic responses.

Some theories require, in a manner at present unknown, all color receptors to respond efficiently to all parts of the spectrum. As an example of these the theory advanced by Wright (*35*) may be quoted. He writes: "The triple sub-division may very possibly occur within the cones on a submicroscopic scale which cannot be revealed by our present techniques." Apart from these theories which postulate that all cones respond to all colors, the remaining theories suppose the receptors to be divided into a certain number of different types. In the case of the three-color theory there are obviously three types; in the case of the polychromatic theory, several types; and so on. Now these theories automatically require that there be different fixation points for different colors, since it is obviously impossible to suppose that a given receptor fixes all colors, both those which come within the range of its response curve and those which do not. Thus, in the case of the three-color theory there must be three different fixation points, one for red rays, one for green rays, and one for blue rays. A four-color theory will correspondingly require four fixation points and so on. Whatever the number may be, several different fixation points would be expected. Such an expectation is derived from first principles and is not directly dependent on the cluster hypothesis, with which it is in complete accord, since the most likely situation for a fixation point, for a particular color, is near the center of a cluster of receptors which respond to that color.

It will be recollected that two different methods were employed by the author (*9*) when determining the positions of the fixation points in the foveal area: (a) the kinesthetic method, which depended on the subjective appreciation of eye movements, and (b) the local scotoma or blind-spot method. These methods gave confirmatory results. That local scotomata are present near the foveal center was first discovered by Franklin (*7*) and was supported by Wilbrand (*32*). That the position of the fixation point is a function of the wave length has been suggested by some experiments performed by Thomson (*31*). This conclusion is substantiated by observations made by the author. It is reasonable, therefore, to accept the hypothesis (a) that there are different fixation points for the different colors, (b) that their positions can be determined by suitable methods, (c) that their positions are a function of the wave length. The author decided that there were 7 different fixation points at a time when he was unaware of the large mass of evidence in favor of the polychromatic theory. These pieces of evidence therefore provide strong support for one another.

Probably the first experimenter to apply the principle of microstimulation to the human retina was Holmgren (*13*), who caused the image of a very small point of light to pass slowly over the surface of the fovea. When the source of light was yellow, Holmgren found that it was seen as red in some positions and as green in others. It was thought at the time that this gave strong support to the tricolor theory, but we now know, in view of the antichromatic responses, that this is not the case. In the same year Fick (*6*) found that if a source of colored light be sufficiently reduced in visual angle, it becomes colorless. He also found that if two or more such sources of the same color be reduced in visual angle until, seen separately, they appear colorless, when seen together their colors are restored. These observations of Holmgren and Fick have been confirmed and extended by the author using the microstimulator in combination with a spectrometer for obtaining monochromatic light. On the basis of the three-color theory it would be expected that, when the image of a small source of white light is caused to move slowly over the surface of the fovea, it would be seen as red in some positions, as green in other positions, and as blue in yet other positions. But in addition to these colors the author has also observed orange and blue-green. When suitable conditioning stimuli are present at the same time, as used by Fick, yellow and violet are also to be seen, making 7 colors in all. This is one more piece of evidence which supports the polychromatic theory.

XI. Some Other Receptor Arrangements

When alternative hypotheses to the polychromatic theory were examined by the author, particular attention was paid (a) to modifications of the three-color theory and (b) to three-channel hypotheses.

One modification of the three-color theory has already been referred to in this address namely, linking between the red and the green receptors at the fovea at high light intensities and at the periphery of the retina, and linking between the green and the blue receptors at the fovea at low light intensities and at small visual angles. Of all the modifications of the classical three-color theory this seemed to the author to be the most promising. It fails, however, mainly for three reasons: (a) it gives no explanation of the changes in shape of the luminosity curve; (b) it gives no adequate account of the differences of color vision between the true trichomats—that is, of subjects with normal sight on the one hand and between the protanomalous and the deuteranomalous on the other; (c) it does not comprise the necessary number of different types of receptor to comply with the requirements of the phases of vision referred to in sections II, III, IV, VII, VIII, and X. In consequence there is no alternative but to abandon this attractive hypothesis.

Of the three-channel hypothesis, one of the best known is that proposed by Granit himself (*8*) soon after his discovery in the mammalian retina of modulator response curves. His suggestion was that the nerve pathways from the orange and the yellow modulators might converge onto a single channel, that the three green modulators might do the same, and similarly for the two blue ones. Thus, there would be polychromatism in the retina but trichromatism in some part or parts of the nervous channels between the receptors and the brain, and possibly in the brain itself. Le Gros Clark (*21*), as the result of a histological survey of the external geniculate body of the monkey, has proposed that this structure forms a part of this triple channel. Now there can be little doubt that this hypothesis is in certain respects an improvement on the preceding one; thus, the polychromatism of the retina offers an explanation of the retinal direction effects which depend on local conditions. It also accounts for the many different fixation points. Important facts which it cannot deal with are spectral mixture, hue discrimination and the essential differences between the normal-sighted subject and the anomalous trichromat, all of whom must use the same three channels if this hypothesis is correct. Apart from these general criticisms there are some special ones, because Le Gros Clark has claimed that the periphery of the retina is dichromatic, with yellow and blue as primary colors. But this is only true at moderate intensities of illumination and ceases to be so if the light intensity is increased. He has also claimed that the fovea is dichromatic, with red and blue-green as primary colors. But in this case also the dichromasy is conditioned by light intensity and disappears, if this be increased. Lastly, the external geniculate body, if Le Gros Clark's description is correct, contains no provision for a channel connecting the rod receptors with the brain. If this does not pass through the external geniculate body, what course does it pursue? These are but a few of the difficulties which beset this three-channel theory.

Of four-color theories, the only one which need claim attention here is that originally proposed by Hering (*12*), because it is representative of the others. The four most likely receptor types have response curves with crests in the red, the yellow, the blue-green, and the blue, but the red receptor also has a subsidiary response in the violet part of the spectrum; in consequence the four types of receptors comprise five response curves. Since the red and the blue-green receptors are complementary, and since the former also acts in the violet, they form a unit which may be identified as the R-BG-R unit of the polychromatic theory. In the same way the yellow and blue receptors of Hering's theory, since they are complementary, may be identified as the Y-B unit of the polychromatic theory. Thus, Hering's theory in a modern form may be regarded as similar to the polychromatic theory, from which the tricolor unit has been omitted. What, then, would be the disadvantages of doing this? For normal foveal vision both units would be in operation. On reducing light intensity or visual angle the Y-B unit would drop out, leaving the R-BG-R unit alone in action. At high light intensities the Y-B unit would be the only effective one. The same unit would operate when there is dichromasy of the retinal periphery. Since these units comprise complementary pairs of receptors, the constancy of white under all these conditions is satisfactorily accounted for. The varieties of color blindness are not so readily explained. Protanopia might be due to the Y-B unit, and deuteranopia to linkage of the yellow and the red receptors to form a single receptor mechanism together with the corresponding linkage of the blue-green and the blue receptors to form the second receptor mechanism. Protanomaly might be caused by linkage of the red and the yellow receptors, the green ones and the blue ones acting separately. Deuteranomaly might be caused by linkage of the green and the blue, the red and the yellow receptors acting separately, and so on. Where the four-color theory fails most obviously is when it attempts to fit in with hue discrimination data.

An examination of other theories leads to the final conclusion that only the polychromatic theory is in agreement with all the known facts, and that this not only must extend along the nervous channels which connect the receptors to the brain but must also apply to the brain itself.

SUMMARY

Until a few years ago it was possible to account for nearly all the aspects of human color perception on the basis of the three-color theory, but such is no longer the case. This is largely due to improvements in the older methods of investigation and to the invention of new ones. Among the latter may be mentioned the microelectrode technique of Granit and the retinal direction effect of Stiles and Crawford. Modern requirements are met by a polychromatic theory, comprising 7 types of receptor, but there is no necessity for these to have such narrow spectral response curves as those exhibited by Granit's modulators. Modifications of the three- and four-color theories have been examined to see to what extent they can be made to fit in with experimental results. Particular notice has been taken of the possibility that there is polychromatism of the retinal receptors, but trichromatism of the nerve paths which connect these to the brain or even of the brain itself.

The conclusion arrived at is that there must be polychromatism throughout the éntire visual mechanism for color perception if a complete account is to be given of all the known facts.

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