THE PERCEPTION OF LIGHT AND COLOUR AND THE PHYSIOLOGY OF VISION

Part VI. Defective Colour Vision

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1. INTRODUCTION

THE subject of defects in colour vision is one of very general interest. The actual nature of the defects, the different types of defect and the relationships between them, the hereditary character of the defects, the frequency of their appearance in the human population and their distribution as between the sexes, the manner in which they can be brought to light and their relationship to occupational fitness are some of its different aspects. The scientific investigation of the characters of defective colour vision is a necessary preliminary to a deeper understanding of its nature and origin. In view of the many-sided nature of the subject, it has naturally been the theme of numerous studies and researches and an extensive literature has grown up dealing with it from different points of view.

In the present memoir, we shall concern ourselves chiefly with the fundamental aspects of defective colour vision. The subject will be dealt with on the basis of the ideas set forth and developed in the preceding parts of the memoir.

2. THE ORIGIN OF THE DEFECTS

The defects of colour vision which we shall proceed to discuss in detail are of congenital origin and belong to the so-called sex-linked and recessive type of inheritable characters. The principles of genetics indicate, in agreement with observation, that defective colour vision should be far less common amongst women than amongst men; usually the woman acts simply as a carrier and transmits the defect without showing any characteristic anomaly herself. The fact that the defects are passed on from parents to progeny is of deep import and suggests that they stand in the closest relationship to the functioning of biochemical processes in the human body. In this connection, it is appropriate here to recall other inheritable characters which are clearly of a biochemical nature. The blood group to which an individual belongs is one of them. Another is the rare condition known as hæmophilia, which is the failure of human blood to stop flowing out from a wound when a person has been accidentally injured. This is known to be a sex-linked recessive defect.

By far the commonest and most thoroughly studied defects in colour vision are those which relate to the perception of the light appearing in the region of the spectrum between 495 $m\mu$ and 780 $m\mu$, in other words those covered by the green, yellow, orange and red sectors in the spectrum as perceived by a person with normal colour vision. In this region, as we have seen, vision is mediated by the two visual pigments ferroheme and ferriheme. These have similar structures which differ only in that the iron atom appearing at the central position of the tetrapyrollic group in one case is in the ferrous and in the other in the ferric state. The question naturally arises as to the nature of the biochemical mechanism which regulates the proportion in which the two pigments appear in the retina. The passage from the ferrous to the ferric state is a change in valency and may be regarded as an oxidative process. It is to be presumed that there is a mechanism at work by which the formation of the ferric pigment is permitted up to a certain proportion and its further progress beyond that point is inhibited.

If the suggestion made above represents the actual position, it follows that the mechanism might, at least in some cases, not function in the normal manner. For example, it is possible that the oxidation is totally inhibited, in which case only ferroheme would be present in the retina. Then again, there might be cases intermediate between such a complete inhibition and the normal functioning of the mechanism. It is also possible that there might be a lack of balance in the opposite direction and some cases in which the oxidation goes so far that ferriheme is in excess of that needed for normal colour vision.

In what follows, we shall consider the consequences of the biochemical situations indicated above and compare them with the actual facts elicited by studies of the different types of defective colour vision.

3. Protanopic and Protanamolous Vision

The cases of defective colour perception which came first under notice and received the largest share of attention were naturally those of the extreme kind which revealed themselves without any special efforts being made to discover them. Subsequently, however, scientific studies showed that the incidence of the defects is larger than was suspected and that there is a considerable variation in the actual magnitude and character of the defects. At the present time, if we leave aside some rarer types, the kinds of colour vision which have been recognized and investigated are five in number: I. Protanopic vision (1%). II. Protanamolous vision (1%). III. Normal vision (92%). IV. Deuteranamolous vision (5%). V. Deuteranopic vision (1%). The approximate percentages of the male human population belonging to these classes have been entered in round figures after each of them. The first and the fifth kinds are usually grouped together as dichromatism, while the second and fourth are commonly referred to as anamolous trichromatism, in other words as variants of normal vision.

We shall first consider protanopic vision. Its characters may be deduced from those of normal colour vision discussed in detail in the fourth part of this memoir. In the absence of ferriheme, the distribution of luminosity in the spectrum, the colour sequence observed and the form of the hue discrimination curve would all be necessarily disturbed. The luminosity would be zero in the sector of the spectrum between 650 mμ and 780 mμ and would be diminished relatively to the rest in the regions of the spectrum where ferriheme, when present, contributes to the observed luminosity. The red sector would disappear completely from the spectrum. In normal vision, ferroheme and ferriheme co-operate in the regions where yellow and orange are seen, and hence in the absence of ferriheme these colours cannot be perceived. Protanopic vision which operates by the mediation of only two pigments, namely, xanthophyll and ferroheme, would accordingly present only two sectors in the spectrum, one on either side of the wavelength 495 mμ which forms the boundary between blue and green in the normal colour sequence. Hence, as in normal vision, that wavelength would continue to be the point in the spectrum where the colour as perceived by the protanope changes most rapidly. The features of the hue discrimination curve observed at greater wavelengths would, however, disappear and be replaced by a continuous falling off in the rate of change of observable colour with wavelength. The features of protanopic vision thus deduced are in agreement with those actually observed. The comparisons between normal and protanopic vision in respect of spectral luminosity and hue discrimination exhibited respectively in Figs. 1 and 2 are based on the observations of F.H.G. Pitt.

We now proceed to discuss the characteristics of protanamolous vision on the assumption that this type of vision results from a replacement of the ferroheme which alone is present in protanopic vision by a small proportion of ferriheme. The effect of such replacement on vision would be principally

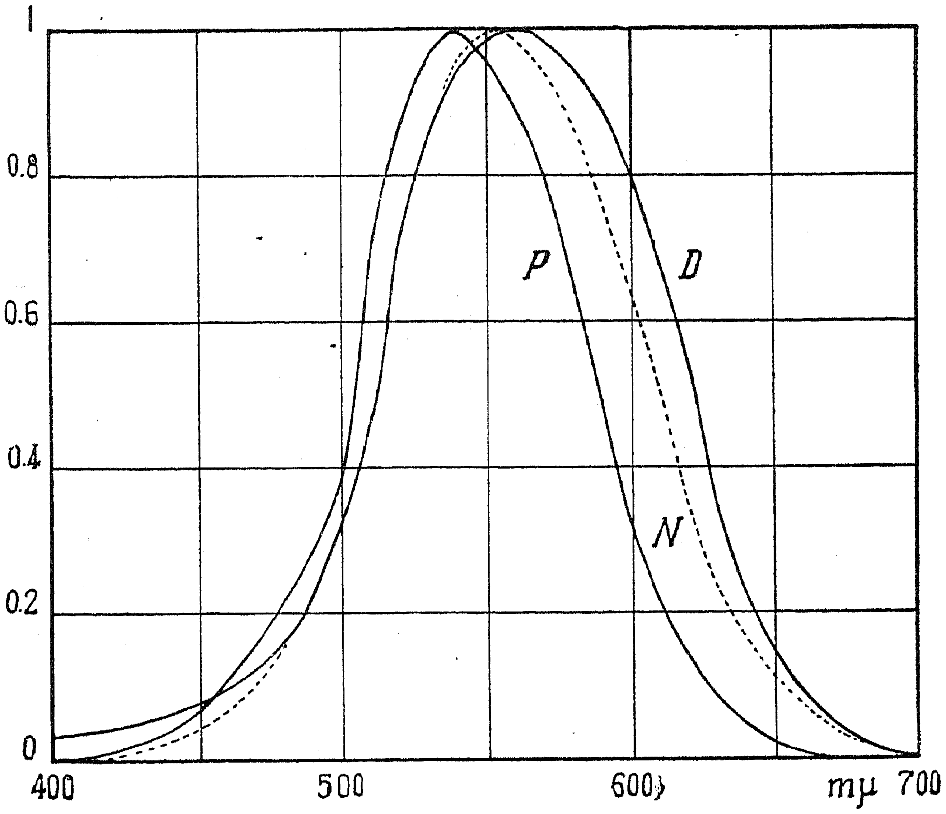

FIG. 1. Comparison of spectral luminosity curves for protanopic (P), deuteranopic (D) and normal vision (N).

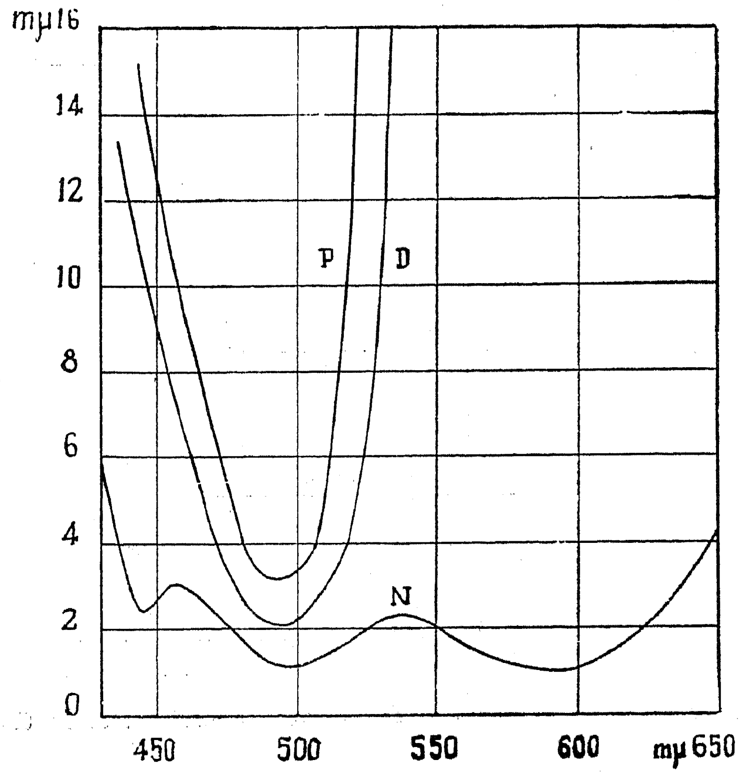

FIG. 2. Comparison of hue discrimination curves for protanopic (P), deuteranopic (D) and normal vision (N).

felt in the region of wavelengths where the absorption of ferriheme is comparable with or actually stronger than that of the ferroheme. This is the region between 560 mμ and 650 mμ where in normal colour vision, green changes over to yellow and then to orange and red. In this region, the protanamolous observer would see hues not perceived by the protanope, and recognise that they alter with the location in the spectrum. In other words, besides the rapid change in colour around 495 mμ which is apparent alike to the normal observer and the protanope, the protanamolous observer would observe colour changes roughly analogous to those apparent to normal vision in the region of wavelengths between 560 mμ and 650 mμ, but of a much less precisely defined character. The greater the quantity of ferriheme which replaces ferroheme, the more clearly would these features be perceived. It may therefore be expected that the protanamolous vision would exhibit in its hue discrimination curves a wide range of variation, approximating to normal colour vision at one end of the range to that of protanopic vision at the other end.

The conclusions reached above find support in the experimental data represented in Fig. 3 below of the hue discrimination curves of four pro-

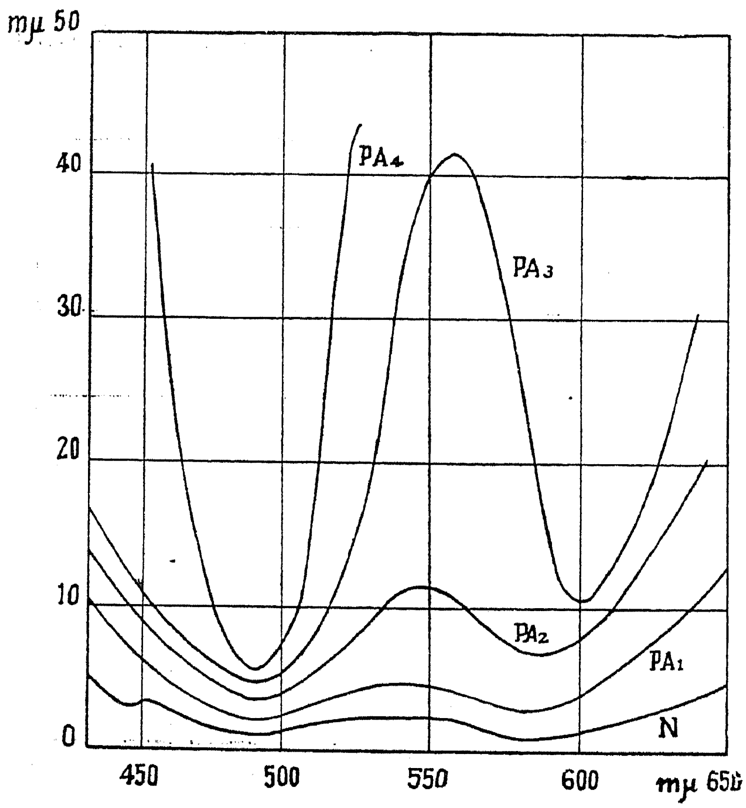

FIG. 3. Comparison of hue discrimination curves of protanamolous (Pa) and normal observers (N).

tanamolous observers and one normal observer which have been selected from the extensive set of data presented in a paper by McKeon and Wright.

4. Deuteranopic and Deuteranamolous Vision

A biochemical situation which results in the presence of an excess of ferriheme over ferroheme would have consequences in respect of colour vision which can readily be foreseen. As the ferroheme-ferriheme ratio diminishes, the region of wavelengths in the spectrum within which the absorptions of the two pigments are of comparable strength would shift towards shorter wavelengths and their overlap would extend and become effective until it completely covers the sector of the spectrum which appears green to a normal observer. In other words, the green and red sectors of the spectrum cease to have a separate existence and merge to form a tract in which the yellow and orange regions which ordinarily form only a fringe between them extend and cover the entire range of wavelengths referred to. Thus, instead of the normal colour sequence of green, yellow, orange and red, a band of colour would appear which may be described as yellow with a greenish tinge at one end and a reddish tinge at the other. This would cover the entire region where the absorption spectra of ferroheme and ferriheme co-operate. It would terminate at about 495 mμ where the blue-violet sector of the spectrum begins. Thus, again, as in protanopic vision, the spectrum consists of only two sectors meeting at about that wavelength. The difference between deuteranopic and protanopic vision is that in the former case, the spectrum goes up to the extreme red end instead of stopping off at shorter wavelengths. The colours observed would also be different in the two cases.

Observational evidence confirming the correctness of the foregoing explanation of deuteranopic colour vision is furnished by the spectral luminosity curves and the hue-discrimination data for several deuteranopic subjects which have been made available by the work of F. G. H. Pitt. These have been represented alongside of those of protanopic and normal observers in Figs. 1 and 2 above respectively in the text. They show very clearly the much greater extension of the spectral luminosity curves towards the red in deuteranopic as compared with protanopic vision. The difference between deuteranopic and normal vision in respect of the spectral luminosity curves is also distinctly shown. The hue discrimination curves, on the other hand, show a general similarity between protanopic and deuteranopic vision and a striking dissimilarity with the normal vision. The observations, however, reveal the noteworthy and significant fact that deuteranopic vision has a distinctly better hue discrimination than protanopic vision in the wavelength range between 400 mμ and 530 mμ. But hue discrimination is completely lacking in the region of greater wavelengths in both types of vision.

We shall not here pause to discuss the results of colour mixing experiments made with observers having one or the other of these two types of defective vision, as also studies of the colour confusions which they exhibit when presented with test objects which appear of different hue to normal observers. These features of protanopic and deuteranopic vision are readily deducible from the fundamental results set forth above. We shall proceed to consider the features of deuteranamolous vision which are of special interest if only for the reason that this type of defective vision outnumbers all the other types put together. Deuteranamolous vision can be distinguished from normal vision by the method of observation by which its existence as well as that of protanamolous vision was discovered, *viz.*, that of requiring the person tested to match a monochromatic yellow by a mixture of monochromatic green and red radiations by varying their relative intensities. A protanamolous observer would require a smaller ratio of green to red than is required for normal vision, while a deuteranamolous observer would need a larger ratio. This is a clear indication that red light appears dimmer in protanamolous than in normal vision, while it appears brighter in deuteranamolous vision. Since protanomaly is explicable as a consequence of the ferroheme-ferriheme ratio being larger than the normal, it may be inferred that deuteranomaly is a result of ferriheme being present in the retina in excess of that required for normal colour vision.

The observable consequences of ferriheme being present in a proportion greater than normal should be of three kinds: (*a*) a shift of the spectral luminosity curves towards longer wavelengths as compared with normal; (*b*) a reduction in the power of hue discrimination at all wavelengths greater than 5000 Å and (*c*) changes of the chromatic coefficients, *viz.*, the intensity ratio between green and red monochromatic radiations of chosen wavelengths which when superposed would match the colours of the spectrum at various wavelengths. In respect of all these features, it may be expected that the magnitude of the observed changes would depend upon the actual proportion of ferriheme present. The more nearly the ferroheme-ferriheme ratio approaches normal, the greater would be the resemblance between deuteranamolous and normal vision. *Per contra*, the greater the excess of ferriheme present, the more would deuteranamolous vision tend to approach deuteranopic vision in its characters.

The observational evidence available supports the foregoing inferences. D. B. Judd in a published report has drawn the individual spectral luminosity

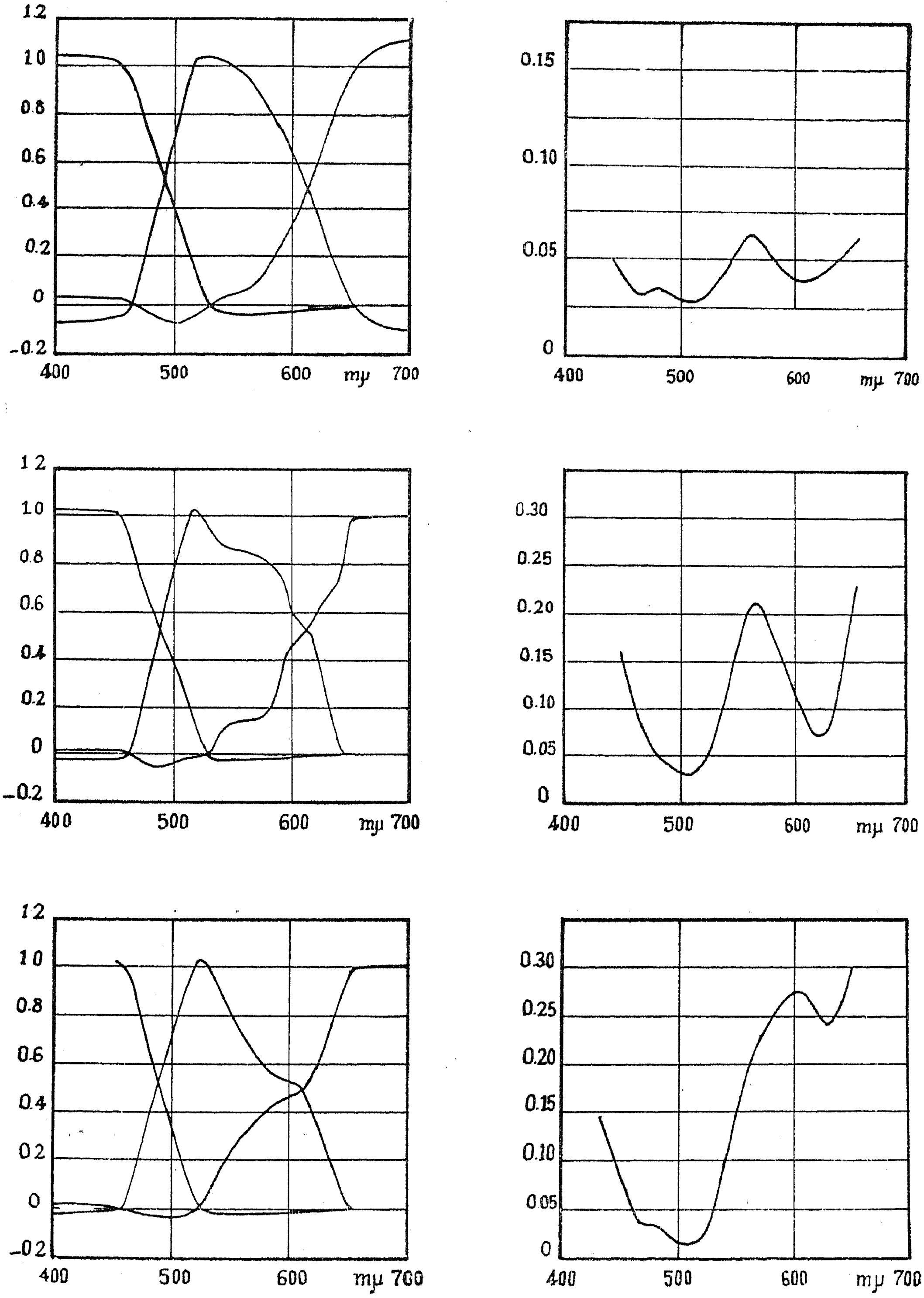

FIG. 4. (*a*) Spectral chromaticity coefficients and (*b*) hue discrimination curves of three deuteranamolous observers according to J. H. Nelson. The unit of the ordinates in Fig. 4 (*b*) is 100 mμ.

curves of twelve protanamolous and of six deuteranamolous observers and compared them respectively with the averages of the luminosity curves of six protanopes and of six deuteranopes. As is to be expected, the luminosity curves of both the protanamolous and of deuteranamolous observers exhibit a certain spread amongst themselves. The significant result emerges that the average curve for the six deuteranopes appears clearly separated and shifted towards longer wavelengths from the region where the individual curves of the deuteranamolous observers are recorded.

The fall in power of hue discrimination and the alterations of the chromatic coefficients are necessarily related to each other. For, the extension of the overlap of the absorption spectra of ferroheme and ferriheme due to the latter being present in excess would obliterate the colour difference between the green and the red sectors of the spectrum. This, on the one hand, would result in a large increase in the limen for hue discrimination and also shift the wavelength where the minimum of limen appears towards the red where there is no such overlap. Simultaneously, the chromatic coefficients for green and red would tend to approach and become equal to each other in the same region where the power of hue discrimination registers a large diminution.

The foregoing inferences find very clear support in the data represented in Fig. 4 where the chromatic coefficients and the hue discrimination curves for three different deuteranamolous observers are shown side by side to exhibit the correlations between them. These have been selected from a more extensive set of observational data published by J. H. Nelson.

5. TRITANOPIA

It has been shown in the third part of this memoir that the carotenoid pigment xanthophyll is the visual receptor in the blue and violet regions of the spectrum. Its absorption which is negligible at wavelengths greater than 520 mμ, rises very steeply around 490 mμ and after reaching fairly high values between 480 mμ and 440 mμ drops down again to relatively small values in the far violet.

It follows from what has been stated that if xanthophyll is totally absent from the retina, colour vision would be seriously affected in the blue-violet sector. In the first place, the observer would be unable to distinguish between the blue and green colours in the spectrum. The luminous efficiency would fall off towards the end of the spectrum rather more rapidly than it would for a normal observer. The hue discrimination curve should also show striking abnormalities. While the usual well-marked minimum of the limen around 590 mμ would continue to be observed, the form of the curve in the green and blue regions would be totally different. The maximum value of the limen observed around 540 mμ and the minimum around 490 mμ would both disappear. Instead, there should be a progressive increase in the limen with diminishing wavelength at all wavelengths less than 590 mμ.

Though tritanopia is usually regarded as a rare condition, a search initiated by W. D. Wright involving the extensive publication of test colour charts resulted in a fairly large number of cases being discovered and investigated. The incidence of tritanopia has been found to be of the order of 1 in 20,000 persons. The indications are that tritanopia is an inherited condition but its incidence amongst women and men is not so widely different as in the cases of the more commonly observed types of defective vision. The consequences of the absence of xanthophyll in the retina indicated above are in general agreement with the findings of W. D. Wright. It was, however, noticed that while the power of hue discrimination virtually disappears in the blue-green wavelengths, it shows a rather surprising recovery near the far-violet end of the spectrum. This would seem to suggest that in the spectral region where the absorption of xanthophyll becomes very small, the other visual pigments ferroheme and ferriheme, play a not wholly negligible part in colour vision and colour discrimination.