extends to seaward. Together with the local tidal streams they may account for the danger of bathing in certain localities; they can sometimes be detected because foam or discoloured water is seen moving outwards through the breakers. It is reasonable to suppose that they are stronger with high waves, especially when a group of high waves is followed by a group of low waves, since the high waves will tend to build up a head of water on the beach. Little is known of the behaviour of breaking waves, but it has been assumed with some success that the wave breaks when the water-particle velocity, which depends on the height of the wave, exceeds the wave-velocity, which depends on the depth of water. Such an argument implies a close relationship between the height of a wave and the depth of water in which it will break; and it has been shown that there is a tendency for waves to break when the ratio of water-depth to wave-height is four-thirds.

Prof. J. D. Bernal gave an evening discourse on "Waves and Beaches" on September 13; all available tickets were issued before lunch-time on the first day of the meetings, and the close attention of the crowded hall showed a lively interest in the subject as well as appreciation of the inspiring lecture. After summarizing the studies made during and since the War, Prof. Bernal described their application to military purposes and the prevention of coastal erosion, and showed how a better knowledge of the transport of sand and shingle by waves would be useful in geological studies. In discussing coastal erosion and other coastal engineering problems, he remarked that no other industry spent such a small proportion of its outlay on research, or stood so much in need of accurate knowledge of the basic principles involved and of some central authority.

MULTIPLE ALLELOMORPHS IN COLOUR VISION

By Dr. R. W. PICKFORD
Department of Psychology, University of Glasgow

EVIDENCE has been found that the main forms of defective red-green colour vision in man are multiple allelomorphs, alternative to each other and to the normal form[1]. In order to prove this hypothesis it would be necessary to show: (*a*) that the forms of red-green vision are discontinuous variations; (*b*) that they are inherited true to type; (*c*) that they segregate independently; and (*d*) possibly that they have an order of dominance. It will be seen that the evidence in favour of the hypothesis is very strong.

Discontinuous Variations

The question is very important whether or not the well-known variations of colour vision, two of which are generally called red-green blindness, are the extremes of a continuous normal curve. Rayleigh[1a] threw doubt on the continuous nature of these variations in 1881. He showed that there were red and green anomalous subjects who were characteristically different from the normal, from each other and from the red-green blind as well. This has been confirmed by Pickford[2]. In addition, Rayleigh indicated in the same paper that the two types of red-green blindness were also distinctively different, a conclusion supported by von Kries and Donders[3] and by Pickford more recently[4]; while Houstoun showed by means of his microscope test[5] that the major red-green defectives formed a small and rather irregular group separated clearly from the large group of normal subjects.

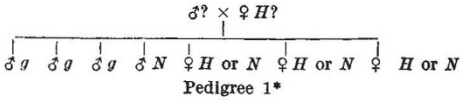
In a recent investigation upon some 900 normal and more than 140 red-green defective subjects (the latter not all found by chance), I have found convincing evidence of a statistical kind that there are four or probably five distinct types of red-green vision in addition to the normal form. This research will be published in full as soon as possible (*J. Psychol.*, in the press). The types are: deuteranope, protanope, green anomalous and red anomalous, the latter being divided into two classes, those with and those without the darkened red of the protanope. Whether the two types of red anomalous subjects are statistically distinct is difficult to decide finally on the basis of the eight cases available, but it is extremely likely.

Adequate tests, which will be published shortly, show that the anomalous subjects are not to be viewed as the intermediates between the red-green blind and the normal. To think of the green anomalous as intermediate between the normal and the 'green-blind', while the red anomalous might be intermediate between the normal and the 'red-blind', is highly tempting. There are, however, grave objections to this: (1) neither class of anomalous subjects is sufficiently variable to fill the gap it is supposed to occupy; (2) both the so-called 'red-blind' and 'green-blind' are, in fact, red-green blind; (3) though most red-green blind subjects are more defective, some are actually less defective than the anomalous, who are possibly to be identified with Houstoun's "colour-different" subjects[6]. Edridge-Green was well aware that the anomalous were not true intermediates[7]. It was only in terms of the Young–Helmholtz theory, now rapidly becoming more and more difficult to sustain[8,9], that they could be thought of as true intermediates; indeed, it has long been realized[10], as Rayleigh foretold[11], that the red-green blind cannot be divided into the 'red-blind' and 'green-blind' classes, but must be divided on the principle that while both types are red-green blind, in the protanopes or scoterythrous the red end of the spectrum is greatly darkened, and in the deuteranopes or photerythrous there is no darkening of the red. That about half of the red anomalous do not have the darkened red of the protanope is a fourth objection to treating them as intermediates.

It is inevitable that we should conclude that there are four (or probably five) types of major red-green vision defects, which are as clearly discontinuous from each other and from the normal as is usual with familiar Mendelian allelomorphs.

Inheritance True to Type

Few people have realized the implications, for the theory of inheritance of colour vision defects, of Rayleigh's pedigree[12] showing the green anomalous condition in three of his brothers-in-law. The seven siblings he tested are shown in Pedigree 1*. The three brothers who were green anomalous inherited the defect true to type, and were completely different



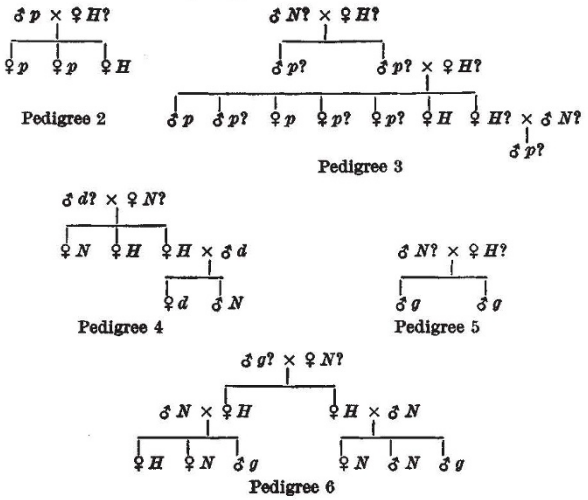
Pedigree 1*

* Throughout this paper N = normal, d = deuteranope, p = protanope, g = green anomalous, r = red anomalous, H = 'normal' heterozygote (see section on heterozygotes later in this article), ? = doubtful owing to inadequacy or lack of testing.

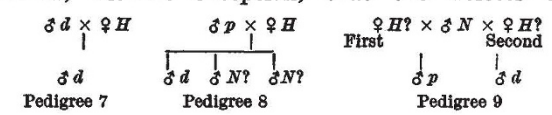
from the other brother, who was normal, and from the sisters, who appeared to be unaffected. This pattern of inheritance fits the Mendelian scheme for a recessive sex-linked allelomorph, which would be for the green anomalous condition in this case.

Several published pedigrees show that the same Mendelian principles apply to the red anomalous condition (protanomaly)[13], to the green anomalous condition (deuteranomaly)[14], to deuteranopia[15], and to protanopia[16], although it is only too well known that some tests in common use have not been above scientific criticism, and that the difficulties of collecting information from relatives for the completion of such pedigrees are always very great.

I have confirmed the implications of these pedigrees in every respect, with the exception of not having had the good fortune to trace the red anomalous condition in the relatives of an affected subject because the relatives were inaccessible. Pedigrees 2, 3, 4, 5 and 6 are good examples taken from a large collection*. All pedigrees which have been collected



show that the defect is inherited in such a way that it is either manifested true to type (whether in a man or in a woman), or does not appear; and that the mode of inheritance is invariably that of a Mendelian sex-linked recessive[17,18]. Other experiments have shown that it is, in fact, an incomplete recessive, since it generally appears in a small and recognizable degree in normal heterozygotes[19]. Even where the defect appears to pass from father to son[20], the sex-linked pattern is not necessarily contradicted, because it is probable that the mother was a heterozygote, and unless this possibility is excluded we cannot be sure of transmission directly from father to son. The fact that I have found the following three pedigrees (7, 8 and 9) shows that the greatest care is needed concerning this point. Finally, I have found, without exception, that the defects are



inherited not only true to type, but also in degree. That is to say, an extreme deuteranope's defective relatives are also extreme deuteranopes, a moderate deuteranope's are moderate, and similarly for protanopes.

* Where there is a query (?), good evidence, though falling short of a perfectly adequate test, indicated the condition.

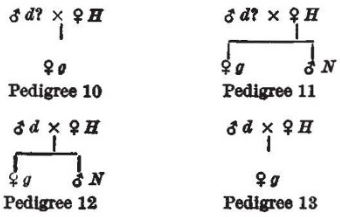
Independent Assortment

The independent assortment of types of colour-vision defect is clearly shown by certain published pedigrees, in spite of the possible inadequacy of the tests used. For example, the independent assortment of the red anomalous (protanomalous) condition and an unspecified form of red-green blindness is shown by a pedigree due to Göthlin[21]. That of the deuteranope and an anomalous condition unspecified is shown by pedigrees due to Guttmann[22], that of the deuteranope and the green anomalous (deuteranomalous) condition by pedigrees due to Göthlin and Wölfflin[23]; while that of the green anomalous (deuteranomalous) condition and an unspecified form of red-green blindness is shown by a pedigree due to Döderlein[24]. Finally, the independent assortment of protanopia and deuteranopia is shown by certain pedigrees in which there are some members with one and some with the other defect[25], and one in which father and son had different defects[26] as in my Pedigree 8. It is most unfortunate that many of the collectors of pedigrees of colour blindness have not realized the importance of specifying exactly the type and degree of defect (if any) of each person tested, and, indeed, even more unfortunate that no adequate test has been available in the past for separating the types with complete certainty. In the absence of an adequate method of measuring their heights, we should never have been certain that short peas were on the average shorter than tall peas by an amount differing to a statistically significant degree from zero. Nevertheless, in colour vision, the evidence favouring the hypothesis of the independent assortment of red-green major defects in general and the normal condition is overwhelmingly great, while that favouring the same hypothesis in relation to the different types of defect among themselves is very great indeed.

Order of Dominance

The most convincing evidence for the theory that the statistically distinct forms of sex-linked red-green colour vision defect are multiple allelomorphs might come from a study of their combinations. These combinations, however, can occur only in women, and any possible evidence concerning the effects of combinations of defective genes in the same heterozygote will be confined to a proportion of the 0·61 per cent[27] of major defective women. The smallness of this percentage makes research very difficult, and shows that it is of great importance that as many red-green defective women as possible should be discovered and persuaded to undergo adequate tests, together with a sufficient number of their male relatives on both sides of the family, to indicate their genotypes conclusively.

In the present investigation, fifteen red-green defective women were tested efficiently, up to the time of writing, and their pedigrees did in four cases give indications of the possible effect of combinations of different allelomorphic genes, though these were unfortunately all of the same kind. They are Pedigrees 10, 11, 12 and 13. In Pedigrees 10 and 11 the fathers had been dead some time; but there was good hearsay evidence from the relatives that they had been (*a*) colour blind rather than anomalous, because the anomalous rarely become noticed for colour mistakes in the family circle, and (*b*) deuteranopes rather than protanopes, because protanopes usually become notorious by confusions relating to red and



black or another dark colour, and in these cases that kind of confusion was not mentioned. In Pedigrees 12 and 13 all relatives were given adequate tests. The four cases all strongly support the view that the daughter was a heterozygote for deuteranopia and the green anomalous condition together, and that the latter was dominant. The possibility that one of the untested fathers was a protanope must be borne in mind, and it would carry with it the implication that the green anomalous condition was still dominant.

In four published pedigrees the underlying principle is the same[28]. All these pedigrees will be found to include a group of relationships such that a green anomalous woman must have been a heterozygote for green anomaly and deuteranopia together, thus again indicating that the green anomalous condition was dominant; and in one of these pedigrees the two conditions segregate independently in the two sons, one of whom is a deuteranope and the other green anomalous.

Four other cases quoted by Bell are also very interesting. One due to Göthlin[29] shows two sons as protanopes, while the father and maternal uncle are both deuteranopes. Here it would not be an unlikely hypothesis that the mother was a protanope heterozygote, inheriting that condition from her father, for her two sons, who must follow the mother, are both protanopes. Another case, also due to Göthlin[30], shows two sons as deuteranopes, two as protanopes and the daughter as normal, while both parents were said to have been normal. A case due to Jeffries[31] shows one son a protanope and the other a deuteranope, while no information is given about the parents. In these two pedigrees the mother might possibly have been a heterozygote for protanopia and deuteranopia together, and, since she was believed to be normal in the one case while no information was given about her in the other, the possibility arises that this particular heterozygote does not differ much from the normal condition, though it is more likely that the defect was not revealed by the tests used. A fourth case, due to Hess[32], shows father and daughter as deuteranopes, though it is not known for what condition the mother was a heterozygote. It is clear that added information in this case would have been most valuable, as in so many others.

Heterozygotes

If it is true that there are five defective allelomorphs for red-green colour vision, then the possible number of genotypes in women will be twenty-one. Of these, one will be the normal homozygote, five defective homozygotes, five normal heterozygotes and ten will be defective heterozygotes. The probable frequencies of these genotypes may be calculated from the observed frequencies of the corresponding defects in men[27], and some would be very rare indeed. It has been shown that the majority of the normal heterozygotes have a small red-green defect[19]. Fuller study of these and of the other combinations would be most valuable.

Conclusion

The hypothesis that there are six multiple allelomorphs for red-green colour vision and its defects in man is supported by the following evidence: (*a*) At least four and probably five different types of red-green sex-linked defect are statistically distinct, namely, deuteranopia, protanopia, green anomaly, red anomaly with and red anomaly without the darkened red of the protanope. (*b*) Many pedigrees indicate that these are inherited true to type, or not at all. (*c*) Many pedigrees show that these types segregate independently. (*d*) Eight pedigrees show that the green anomalous condition is dominant to that of the deuteranope, while all the defective forms are recessive to normal red-green colour vision.

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[12] Rayleigh, *op. cit.*, 65.
[13] Bell, Julia, *The Treasury of Human Inheritance*, 2, *Anomalies and Diseases of the Eye* (1933), Plate XLI, pedigree 595.
[14] Bell, *op. cit.*, Plate XLI, pedigrees 591, 597, etc.
[15] Bell, *op. cit.*, Plate XXXVI, pedigree 513, and Plate XXXVIII, pedigree 565.
[16] Bell, *op. cit.*, Plate XXXVI, pedigree 511, and Plate XXXVII, pedigree 526.
[17] Ford, E. B., "Genetics for Medical Students", 44–6 (1946).
[18] Crew, F. A. E., "Genetics in Relation to Clinical Medicine", 47–8 (1947).
[19] Pickford, R. W., *Nature*, **153**, 409 (1944); **160**, 335 (1947); and Ford, *op. cit.*, 151.
[20] Bell, *op. cit.*, Plate XXXVII, pedigrees 516, 521, 544.
[21] Bell, *op. cit.*, Plate XLI, pedigree 593.
[22] Bell, *op. cit.*, Plate XLI, pedigrees 596 and 599.
[23] Bell, *op. cit.*, Plate XLI, pedigrees 598 and 601.
[24] Bell, *op. cit.*, Plate XLI, pedigree 600.
[25] Bell, *op. cit.*, Plate XXXVI, pedigree 512, and Plate XXXVII, pedigree 527, and Plate XXXVIII, pedigree 563.
[26] Bell, *op. cit.*, Plate XXXVIII, pedigree 551.
[27] Pickford, R. W., *Nature*, **160**, 335 (1947).
[28] Bell, *op. cit.*, Plate XLI, pedigrees 594, 598, 600 and 601.
[29] Bell, *op. cit.*, Plate XXXVI, pedigree 512.
[30] Bell, *op. cit.*, Plate XXXVII, pedigree 527.
[31] Bell, *op. cit.*, Plate XXXVIII, pedigree 563.
[32] Bell, *op. cit.*, Plate XXXVIII, pedigree 565.

OBITUARIES

Prof. Alan F. C. Pollard

FEW people in the world of science and engineering have had such a strong sense of order and direction as Alan Faraday Campbell Pollard, who died suddenly at the age of seventy years at Thames Ditton on August 15. He was essentially a crusader, and his sense of mission was such that he spared no amount of trouble and effort to further the objects in which he so optimistically believed. He will perhaps be best remembered both for his efforts to reform methods of instrument design on a sound scientific basis, and not less for his untiring advocacy of comprehensive schemes for indexing scientific literature and, in fact, all serious knowledge. He was fortunate that in these things he seemed, comparatively late in life, to find his true *métier*, when the very varied experiences of his earlier days had given him a foundation on which to build.