COLOUR BLIND FEMALES:
The Inheritance of Colour Blindness in Man

BY

INGOLF SCHIÖTZ,
ASSISTANT OPHTHALMIC SURGEON, RIKHSOPITALET, CHRISTIANIA.

Medical literature has so far but rarely touched upon colour blindness in females; it is true, that the subject is practically of little interest, but theoretically the occurrence of red-green blindness as an hereditary character is of great importance.

Since the extensive statistics of 1870-1880 little research work has been published concerning the colour sense of women, and I have found very few papers on the subject undertaken with the superior clinical tests of colour sense, which we command at the present time. Since the spring of 1918 I have therefore undertaken a series of such investigations on schoolgirls, having been guided in my choice of tests by the results previously obtained in my investigations on the same subject, carried out in March, 1918. The following six tests have been used: Stilling, Podestà, Nagel, Cohn, Holmgren, Daae.* The tests showed, that out of 332 recruits 37, i.e., 11.2 per cent. were dichromatics or anomalous trichromatics, as seen from the following table.**

<table>
<thead>
<tr>
<th></th>
<th>Stilling</th>
<th>Podestà</th>
<th>Nagel</th>
<th>Cohn</th>
<th>Holmgren</th>
<th>Daae</th>
</tr>
</thead>
<tbody>
<tr>
<td>37</td>
<td>37</td>
<td>31</td>
<td>27</td>
<td>20</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>4 df.</td>
<td>4 df.</td>
<td>5 df.</td>
<td>4 df.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2 +</td>
<td>6 +</td>
<td>12 +</td>
<td>17 +</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

** — not passed, df. = doubtful, + = passed.
The figures are in accord with those found by others, e.g., E. Franke, and with impressions gained by clinical examinations on colour sense. The colour sense was tested in 4 schools, the investigation including 1,270 girls at the age of 10—14 years. Stilling's pseudo-isochromatic tables were used as the main test, and those of Podestà and Nagel for further tests in all cases where Stilling was not read quickly and correctly. Finally, as many as possible of those showing a deficient colour sense, and a number of the doubtful cases, were tested with spectral colour mixtures. At this secondary examination the pseudo-isochromatic tables, arranged by S. Ishihara (Tokyo) were used together with Stilling's test. These tables are somewhat similar to those of Stilling and are very efficient.

Among the 1,270 girls, 11 were found to have a perception of colour so widely different from the normal, that they had to be declared as having "a deficient colour-sense" (4 dichromatics and 7 anomalous trichromatics). There were also a number of doubtful cases, which could not be classified accurately by the clinical tests mentioned above. Twelve of these were therefore selected and tested by means of spectral colour mixtures, the result being, that only one turned out to be a typical deuteranomalous, while the 11 others showed perfectly normal conditions with regard to a series of colour equations. The anomaloscope of Nagel was not at our disposal, but a modified Helmholtz apparatus for colour-mixing and a spectral apparatus made by Hj. Schiötz after Tscherning's model. These apparatus are as easy to use as the anomaloscope, and they are, if possible, more accurate, as they allow an investigation of the reaction of each person to a number of various colour equations. The equations employed were chiefly those given by B. Malling in his first work on colour-sense investigation, viz., in all cases a red-green equation (Rayleigh's equation). Many were tested with a blue-green equation and a white equation (of blue and yellow), and an endeavour was made to fix "the neutral point."

The investigation of school-girls' colour sense was continued in the autumn of 1919 on 930 girls at three private schools. This time the colour-sense was tested exclusively with Stilling's and Ishihara's colour tests, and 3 were revealed as being red-green blind to a considerable degree (dichromatics?), 6 to a lesser degree (anomalous trichromatics?). Besides, there was also a number of doubtful cases, which, however, after renewed testings must be considered as having normal colour-sense.

The two series thus include 2,200 girls with a total of 20 = 0·91 per cent. showing a deficient colour sense," or more specifically 7 deuteranopes and 13 deuteranomalous girls. In the case, however, of such a rare anomaly as colour blindness in females, these figures are too low to be regarded as a final value (and
besides, spectral colour equations were not sufficiently employed). All the same, the figures are not too low for a comparison with my results of similar investigations of men's colour sense, undertaken with the same tests.

During the last two years I have examined more than 2,000 males, and with the tests of Stilling, Podestà, Ishihara, and Cohn, I have found a total of 202 "with defective colour perception" (dichromatics and anomalous trichromatics), viz., out of

<table>
<thead>
<tr>
<th>Total</th>
<th>332 recruits</th>
<th>...</th>
<th>37 with defective colour-sense</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>633 schoolboys</td>
<td>...</td>
<td>66 &quot; &quot; &quot; &quot;</td>
</tr>
<tr>
<td></td>
<td>1,040 applicants for railway posts*</td>
<td>...</td>
<td>99 &quot; &quot; &quot; &quot;</td>
</tr>
</tbody>
</table>

Total 2,005 cases examined with 202 = 10.7 per cent. with defective colour-sense.

The result of these investigations should be, that in this country the proportion between the number of red-green blind males and females should be about ten to one. This is in accordance with other statistics; but to obtain a fairly homogeneous material, which can be used for comparison, it is necessary to go back to the extensive statistical work carried out during the years 1870-80, when Holmgren's wools were used alone to a great extent at the examination of colour sense both in males and females. After that time clinical colour tests have improved and multiplied, so that the actual percentage has steadily risen, as was naturally to be expected. Thus in 1855 George Wilson found 65 colour blind among 1,154 men (5.6 per cent.); Hjalmar Schiötz, 31 colour blind among 485 school boys with O. B. Bull's colour test (6.4 per cent.), and in 1914 H. Köllner, using Nagel's anomaloscope, found that up to 20 per cent. of males gave a colour perception different from the normal; but, perhaps, about one-half of these deviations are so slight, that they would never be of any importance in practical life.

In 1878, A. Daae, using Holmgren's wool-test, found:
Out of 205 boys, 10 colour blind, i.e., 4.88 per cent.
Out of 208 girls, none colour blind

In 1882, Lyder Borthen, with the same test, found:
Out of 423 boys, 15 colour-blind, i.e., 3.5 per cent.
Out of 117 girls, 1 colour blind.

The extensive collection of statistical material carried out in Sweden by Frithiof Holmgren, with his own wool test must be considered very reliable:
Out of 32,165 men, 1,019 were colour blind, i.e., 25 per cent.

* The 1,040 railway applicants had not previously been tested. During the same period, 1,167 employees were tested, who had been tested before in other places and by other methods, some of them several times. Among these, 64 had a deficient colour-sense, i.e., 5.5 per cent. (among them several dichromatics).
Out of 7,119 women, 19 were colour blind, i.e., 0.26 per cent.

I will quote the following figures from O. E. de Fonteney’s work, chiefly made by Holmgren’s method:

Out of 5,287 men, 189 were colour blind, i.e., 3.57 per cent.
Out of 3,663 women, 16 were colour blind, i.e., 0.43 per cent.

A. Schmitz, working with an early edition of Stilling’s pseudoisochromatic tables, found:
Among 2,215 men, 163 colour blind, i.e., 4.6 per cent.
Among 1,485 women, 5 colour blind, i.e., 0.33 per cent.

In the “Report of the Committee on Colour Vision, 1890-92,” the following figures were stated:
Out of 10,846 men, 617 were colour blind, i.e., 4.156 per cent.
Out of 489 women, 2 were colour blind, i.e., 0.41 per cent.

Putting all these statistics together, we find a total of:
51,140 men, of whom 2,013 were colour blind, or 3.94 per cent.
13,090 women, of whom 43 were colour blind, or 0.33 per cent.

That is to say, there were nearly 12 times as many colour blind men as women.

In Joy Jeffries's book the following collective figures are to be found:
55,672 men, of whom 1,900 colour blind, or 3.4 per cent.
19,842 women, of whom 40 colour blind, or 0.2 per cent.

But these two statistics cannot be transformed into one, partly because Jeffries does not describe the tests employed, and partly because in all probability his statistics include some of the figures already quoted.

From the above it is evident that in the years 1870-80 red-green blindness was fairly evenly distributed in the various countries, and the same would undoubtedly be found to be the case at the present time. When, therefore, we find, that in Norway about 10 per cent. of men and nearly 1 per cent. of women are dichromatics or anomalous trichromatics, I have no doubt that similar figures would be found in other countries, if similar investigations with the same tests were carried out.

Some statistics appear to indicate red-green blindness as being more frequently found among Jews than among other races. Thus Cohn and Magnus in their paper of 1878 state, that they found 4.1 per cent. colour blind Jewish boys and only 2.1 per cent. among boys of other nationalities. “The London Committee” found 4.9 per cent. to be colour blind out of 949 Jewish boys, while out of 14,000 non-Jews the percentage was only about 4 per cent.

The question of colour blindness as relative to race, and the colour perception of primitive races is a very interesting one; Favre’s paper should be called to mind on this point, as he refers to results obtained by a colleague in Algeria, viz:
COLOUR BLIND FEMALES

Out of 203 Kabyles ... ... 5 colour blind.
" " 95 natives of Biskra  4 " 
" " 81 Negroes ... ... 1 " 
" " 62 Italians ... ... 1 " 
" " 23 Jews ... ... 1 " 
" " 12 Maltese ... ... 1 "

Rivers during his many travels carried out a number of investigations of the colour-sense. Among others he tested 80 natives of Upper Egypt, four of whom were red-green blind and made the characteristic mistakes with Holmgren’s wools. Further, by the same test he found 43 definitely colour blind among 503 Todas, a hill-tribe of Southern India, while of 150 natives of Murray Islands in New Guinea not one confused red and green; but blue and green and blue and violet were constantly confused. The last fact might be taken to support the theory held by some who maintain that primitive races have a perception of colours less developed than our own, but on this point Meyer is undoubtedly right when he says: “Language affords no safe clue to sensibility. A colour name occurs when it is needful; where it is needless it will not be formed, be the sensibility to that colour ever so great. If we are to gauge the colour sense of a people by colour nomenclature, nearly every primitive people must be dubbed ‘brown blind’ or ‘brown weak’ in as much it is very rare to find a special word for brown.”

This is very well illustrated by what J. H. Parsons writes in his book on Colour Vision: “Two companies of Nubians were travelling about in Germany in 1877, and were examined by Virchow and others. It was found that they used the same word for blue as for black and other dark colours, yet they sorted coloured papers and wools correctly.”

Finally, Hirschberg in his History states, “If any one, like myself, has an opportunity of seeing an Egyptian cave mausoleum just opened after at least 4,400 years, he will, when seeing the gorgeously coloured pictures and hieroglyphs, quickly be convinced that the men who lived 1,500 years before Homer, possessed a perception of colour equal to our own, and more especially, they also perceived blue.”

The statistical side of the problem of colour-sense is important enough, and an examination of the efficiency of the clinical tests is of great practical value. Still more interesting, however, is the study of red-green blindness as an hereditary character.*

Perhaps no other branch of medical science offers a better field for the investigations of hereditary characters than ophthalmology,

*The author wishes to express his indebtedness to Dr. O. L. Mohr, who was kind enough to revise the genetic part of the manuscript.
partly because the ophthalmologist employs very exact methods of investigation, and partly because ophthalmology includes a number of anomalies and defects which have been and are considered hereditary (see Nettleship's very extensive research work, published in Trans. of the Ophthal. Soc., 1902-1912).

The basis of our exact knowledge of the hereditary mechanism was first laid down by the Austrian Abbot, Gregor Mendel (1822-1884). His work was published in 1865, but it was not until after 1900 that the enormous importance of the work was recognized.

The fundamental principle of the Mendelian laws of heredity is the fact, proved by Mendel, that hereditary characters, which are brought together at fertilization, do not lose their independence. In following generations they will separate again, or, as this phenomenon technically is termed, segregate.

It is superfluous to mention that the hereditary material is carried from one generation to another by the sex cells.

These cells, the ripe sperm as well as the ripe egg, are termed gametes, the product of their union, i.e., the fertilized egg, is called a zygote. The gametes transmit the hereditary material from one generation to the other, i.e., they do not transmit the characters themselves, but they contain the corresponding hereditary factors or "genes." Each gamete carries one gene for the character in question, and when the gametes unite at fertilization, the zygote consequently will receive two genes for the same character. These two genes may be identical, and in this case the zygote—and the individual developing from this zygote—is said to be homozygous. But the two genes, which are brought together at the union of the gametes, may also be of different sort. The zygote—and the individual—is then said to be heterozygous for the gene in question.

Of two contrasted characters meeting at fertilization one may appear in the offspring, thus suppressing the other, and this character is said to be dominant, while the other is termed recessive.

An example will make this relation clear, and we may use the inheritance of eye colour in man as an illustration of the Mendelian principle of segregation. As is well known, in ordinary blue eyes only the retinal layer of the iris contains pigment; when pigment also is present in the stroma of the iris, the eye will represent a brownish iris colour. It has now been proved, that the pigmentation calling forth the brown colour, depends upon the presence of a dominant gene. Such dominant gene is, as a matter of convenience, marked by a capital letter, and in our case we can for instance take B (brown). The corresponding recessive character, in this case lack of pigment in the stroma, is marked with the corresponding small letter, here, b. When therefore a brown-eyed individual receives the gene for pigmentation from both parents, then he is homozygous for this character. The formula for the colour of his eyes will accordingly be
COLOUR BLIND FEMALES

BB, the zygote receiving one B from the sperm and one B from the ripe egg. Six possibilities will occur:

I. If both parents are brown-eyed with the formula B B, the formulae of their gametes will accordingly be B, and all their children must become brown-eyed and homozygous.

II. If both parents have blue or grey eyes, i.e., the formula b b, all gametes will have the formula b, and the formula of the offspring will be b b, that is to say, all the children will have grey or blue eyes, and are with regard to the colour of the eyes homozygous, like their parents.

III. If the parents' formulae are B B and b b the gametes will be B, B and b, b

The offspring will have the formula Bb; the children will be heterozygous and because brown (B) is dominant they will all be brown-eyed.

IV. If both parents are heterozygous with regard to the colour of the eyes, having both the formula Bb, their gametes will be B and b and the following combinations will occur:

Gametes:      \[
\begin{array}{ccc}
B & b & \text{and} & B & b \\
\end{array}
\]

Zygotes:      \[
\begin{array}{c}
BB \\
Bb \\
bB \\
bb
\end{array}
\]

Because the gene for pigmentation is dominant, three children should have brown eyes, one being homozygous (BB) and the two others being heterozygous (Bb). For an external examination they will be like each other, but genetically they are of different constitution, which may be controlled in their descendants. The fourth child should from a theoretical point of view necessarily have blue eyes and be homozygous (bb).

V. If one parent has the formula Bb, and the other bb, the following combinations will be possible:

Gametes:      \[
\begin{array}{ccc}
B & b & \text{and} & b & b \\
\end{array}
\]

Zygotes:      \[
\begin{array}{c}
Bb \\
Bb \\
bb \\
bb
\end{array}
\]

that is to say, half the children will be heterozygous, with brown eyes (Bb), the other half homozygous, with blue eyes (bb).

VI. A homozygous brown-eyed individual (BB) with a brown-eyed mate (Bb) will breed brown-eyed children only, one half being homozygous (BB) and the other half heterozygous (Bb).

From the above it will be seen that parents with brown eyes may very well have blue-eyed children, and that this depends upon
the genetical constitution of the parents. Blue-eyed parents, however, cannot produce children with brown eyes, they being always homozygous and always giving gametes free from the gene for pigmentation. Persons exist, however, having one brown eye and one blue, or one eye brown flecked, and this fact may be due to circumstances which prevent the pigment from developing in the eye.

With our present state of knowledge the genes are carried by the chromosomes, small rod-shaped or V-formed bodies, contained in the cell-nucleus. With one exception these chromosomes are, in the body cells, arranged in pairs, i.e., they form two homologous series, according to size and form.

During the ripening of the germ cells these two series separate so that the sex cells only contain one of these homologous series; and the segregation takes place at the so-called reduction-division, which occurs during the maturation of the eggs and sperms. In this division the two members of each chromosome-pair separate so that each daughter-cell only receives half as many chromosomes as the other cells of the individual. From these daughter-cells are formed the eggs and sperms.

The exception mentioned above relates to a single pair of chromosomes, which is only in the female present as a pair, while the male in his cells has but one member of the said pair. These chromosomes are called the sex-chromosomes or the X-chromosomes.

Since the female has two X's in her cells, each daughter-cell originating from the maturation or "reduction"-division mentioned, will receive one X. Since the male cells only contain one X-chromosome, this element will, at the maturation-division of the male sex-cells, pass undivided to one of the two daughter-cells. The other will receive no X-chromosome. Accordingly two kinds of spermatozoa are formed, one half containing an X-chromosome, the other half without such an element.

At the fertilization accordingly two possibilities present themselves. An egg, which always contains an X, may be fertilized by a sperm also containing an X-chromosome. In this case the offspring will receive two X-chromosomes and be a female.

If, on the other hand, the egg is fertilized by a sperm without an X-chromosome, the offspring will only receive the single X-chromosome of his mother and be a male.

<table>
<thead>
<tr>
<th>Egg</th>
<th>Sperm</th>
<th>Zygote</th>
</tr>
</thead>
<tbody>
<tr>
<td>X</td>
<td>X</td>
<td>XX (♀)</td>
</tr>
<tr>
<td>X</td>
<td>O</td>
<td>XO (♂)</td>
</tr>
</tbody>
</table>

The correctness of this chromosome theory of the determination of sex, first fully worked out by E. B. Wilson (1905-06), may now
COLOUR BLIND FEMALES

be regarded as sufficiently established through an abundance of cytological and genetic evidence.

In man, which for our present purpose is of particular interest, the female cells, according to the results of de Winnewarter, contain 46 + 2 X-chromosomes; the male cells 46 + 1 X. Accordingly all the eggs contain 23 + X, and the sperms are of two types, one half containing 23 + X, the other half only 23 chromosomes.

At the fertilization the following two possibilities are open:

\[
\begin{align*}
\text{Egg} & \quad (23 + X) + \quad \text{Sperm} \\
& \quad (23 + X) = 46 + 2 X \quad \text{the female chromosome number} \\
& \quad (23 + X) + \quad 23 = 46 + 1 X \quad \text{the male chromosome number}
\end{align*}
\]

In spite of the extensive work during the 19th century on red-green blindness as an hereditary character, it was very difficult to understand, how this anomaly was inherited, why it may disappear in one or more generations only to re-appear later on. Other features in the hereditary type of the anomaly were also quite inexplicable, e.g., that there are about ten times more colour-blind men than women, and that colour-blind men never have colour-blind children, unless they have married a woman with the hereditary predisposition. It should be mentioned in this connection that an explanation of the peculiar sex-linked inheritance of colour blindness in man, conforming with the chromosome-theory of sex-determination, was already put forward by E. B. Wilson.

If we assume that colour blindness is a recessive character in Mendel's sense, and that the gene for colour blindness is carried by the sex chromosome, then every obscure feature in its inheritance becomes perfectly clear.

A colour blind man carries, on this assumption, in his single sex-chromosome the gene for this anomaly. When he marries a normal woman, his daughters will receive one affected sex-chromosome from himself (their father) and one normal sex-chromosome from their mother. Since colour blindness is a recessive character, the anomaly will not manifest itself in these females, the dominant gene for normal colour sense being present in their other sex-chromosome. Such a woman will therefore herself have a normal colour sense, but nevertheless, if married to a normal man, be able to transmit the gene for colour blindness to half of her sons and half of her daughters, (she will be a "conductor.") Of these the daughters will be like their mother, since the action of the recessive gene for colour blindness is counteracted by the normal sex-chromosome, which they have obtained from their mother (they are conductors).
The sons mentioned will be colour blind, since their cells contain but one sex-chromosome, and in this case an affected one.

A red-green blind woman must necessarily have received the hereditary gene from both parents. Both her sex-chromosomes must carry the gene causing colour blindness, and the sex-chromosome contained in her eggs will be of the same affected type.

A character of this type is accordingly transmitted from the affected grandfather through his apparently normal daughters to half of his grandsons, as was first clearly pointed out by Horner in 1876.

Characters, which show this type of criss-cross inheritance, are called sex-linked characters. Several cases are known from experimental genetic work, and in man the hereditary red-green blindness, a certain form of night blindness, familial atrophy of the optic nerve (Leber's disease), and haemophilia belong to this group.

In the following we will more closely consider the hereditary type of colour blindness and the various combinations of the possible marriages between affected and normal individuals.

If we denote the recessive gene for colour blindness by little c and the corresponding dominant gene for normal colour vision by big C, then a normal female will be of the constitution C C a normal male of the construction Co, the zero indicating that he, having but one sex-chromosome in his cells, may only carry the gene for colour sense in one dose.

In marriages involving individuals of which one or both carry the gene for colour blindness, the following five possibilities are open:

I. A red-green-blind man (c o), marrying a red-green-blind woman (c c), will have red-green blind children only.

female gametes c ; c
male " c ; o
female zygotes c ; c
male " k ; o

II. When a female conductor (C c) marries a colour blind (c o), half of the sons and half of the daughters will be colour blind:

female gametes C ; c
male " c ; o
female zygotes: C c (conductor) and c c (colour blind).

male : Co (normal) and c o (colour blind).

III. A red-green blind man (c o) and a normal woman (C C) will have normal children only, all daughters, however, being conductors.

female gametes C ; C
male gametes c ; o
female zygotes: C c (conductor)

male " C o (normal)

IV. A normal man (C o) and a red-green blind woman (c c) will have red-green blind sons only, all daughters will receive the
COLOUR BLIND FEMALES

Gene for colour blindness in single dose and will accordingly be conductors.

female gametes c ; c
male " C ; o
female zygotes C c (conductor)

male " c o (colour blind)

V. A normal man (C o) and a conductor (C c) will produce sons of which half are red-green blind, and half normal; all daughters will be apparently normal, but half of them will be conductors.

female gametes: C ; c
male " C ; o
female zygotes: C C (normal) and C c (conductor)

male " C o " and c o (colour blind)

On the assumption that these rules are constant, and that the statistical material concerning colour blindness is approximately correct and sufficiently extensive, it should be possible to calculate how often these different types of matings occur, and also how many females are conductors. It is also possible from the percentage of colour blind men to calculate how many colour blind women there are, and vice versa.

As stated above, a male is not colour blind unless his mother is either colour blind or a conductor, and it is easy to calculate how many conductors would be needed in order to produce the 10 per cent. of colour blind men. The percentage of colour blind women, as mentioned above, was about 1 per cent., and they would produce about 1 per cent. of colour blind men, as all their sons would inherit the anomaly.

Conductors transmit the anomaly to half of their sons only, wherefore there would be needed about 18 per cent. conductors to produce the remaining 9 per cent. of colour blind males. This figure is startlingly high, but perhaps not far from actual truth.

Using the 10 per cent. males as a starting point, the number of colour blind women may be estimated. It should be recalled that colour blind female offspring can only be expected in the following marriage-combinations: c c + c o (all daughters colour blind) and C c + c o (half the daughters colour-blind).

How often do these combinations occur?

Because there are 10 per cent. of colour blind men, a woman's chance of marrying such a man is \( \frac{1}{10} \) and if a percentage of 18 is assumed for female conductors, a man's chance of marrying such a woman is \( \frac{1}{5.5} \left( = \frac{18}{100} \right) \). The probability of a marriage where the man is colour blind and the woman a conductor may, therefore, be
estimated as being $\frac{1}{55}$ (1.8 per cent.), and according to the above
(alternative II), in principle half the number of daughters in such a
marriage would be colour blind, and our calculations must lead to
0.9 per cent. for colour blind women.

To these would have to be added the female offspring of all
marriages between two colour blind persons, a combination which
probably does occur in 0.1 per cent. of all marriages. These would
make another 0.1 per cent. of colour blind women, which added to
our previous 0.9 per cent. make 1 per cent., a result which is fairly
well in accordance with the results of the statistics dealt with above.

The author wishes to express his gratitude to Dr. G. H. M.
Waaler, who has been kind enough to control these results from a
mathematical point of view.

Dr. Waaler writes as follows:

"The author has requested me to discuss mathematically the
problem of colour blindness on the assumption that the genetic
principles discussed above are reliable in case of a recessive sex-
linked character.

With regard to colour blindness, mankind is divided into five
varieties, viz.:

1. Normal men ($m_0$), who in the following will be assumed to
form $u$ per cent. of all men:
2. Colour blind men ($m_1$) = $x$ per cent.
3. Normal women ($f_0$) = $v$ per cent.
4. Female conductors ($f_1$) = $y$ per cent.
5. Colour blind women ($f_2$) = $z$ per cent.

The six possible marriage-combinations in any population would
be the following:

<table>
<thead>
<tr>
<th></th>
<th>$m_0$</th>
<th>$f_0$</th>
<th>$m_1$</th>
<th>$f_1$</th>
<th>$m_1$</th>
<th>$f_2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>I.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>III.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>IV.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>V.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VI.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

the total of all these possibilities being 1.
Our problem is to find the mathematical relations between the said five frequencies, more especially for colour blind men (x per cent.), female conductors (y per cent.) and colour blind women (z per cent.).

Let us assume that the percentage keeps invariable through several generations, as it presumably does in a large city; moreover, that colour blind individuals are as fertile as normal ones, and finally that no selection will take place.

Beginning with colour blind women, representing half the daughters resulting from the marriages of type V. and all daughters in marriages of type VI, we get the following formula with regard to the percentage of z:

\[
\frac{z}{100} = \frac{1}{2} \cdot \frac{x}{100} \cdot \frac{y}{100} + \frac{x}{100} \cdot \frac{z}{100}
\]

\[
z = \frac{x}{100} \cdot \left( \frac{y}{2} + z \right) \quad \text{(1)}.
\]

In the same manner the percentage of colour blind men may easily be expressed as follows:

\[
x = \frac{1}{2} \cdot \frac{u}{100} \cdot \frac{y}{100} + \frac{1}{2} \cdot \frac{x}{100} \cdot \frac{y}{100} + \frac{u}{100} \cdot \frac{z}{100} + \frac{x}{100} \cdot \frac{z}{100},
\]

\[
x = \frac{1}{2} \cdot \frac{y}{100} \cdot (u + x) + \frac{z}{100} \cdot (u + x) \quad \text{or, as } u + x = 100,
\]

\[
x = \frac{y}{2} + z \ldots \ldots (2)
\]

From (1) and (2) we obtain the simple formula:

\[
z = \frac{x^2}{100} \ldots \ldots (3)
\]

If a similar equation were constructed for y (i.e., the frequency of female conductors), and a solution were sought with regard to the three unknown values, the three equations would be found to be identical, that is to say, there is an infinite number of sets of values for the three frequencies (x, y, and z). If, however, one of these values is definitely known, the equations (2) and (3) enable us to find the other two corresponding values.

Thus assuming the value found by the author for colour blind men as being the most reliable (x = 10.07 ± 0.45) \( \frac{x}{100} = 1.01 \text{ per cent.}, \) and colour blind women — should be = \( \frac{10.07^2}{100} = 1.01 \text{ per cent.}, \) and
the female conductors, \[ \frac{y}{x} = 2 (x - z) = 18.12 \text{ per cent.} \] 
(calculated by (2)).

Now out of 2,200 women 20 have been found to be colour blind, which represent a percentage of 0.91 ± 0.14, which accords very well with our calculation.

From a purely mathematical point of view such a set of values 1.01 – 10.07 – 18.12 should remain constant for an infinite future, and it is probable that it has existed for a considerable period.

From the above reflections we may be justified in drawing the conclusion, that the values obtained by the collective statistics in 1870-80, viz., 3.94 per cent. colour blind men and 0.33 colour blind women, may be explained through insufficient testing methods, as such relative values could not possibly co-exist in any population, still less remain stationary. On the assumption, that these values were correct, the number of colour blind women in the next generation would be reduced to 0.15 per cent., and the only factor which might keep up a percentage of 0.33 would be a relatively high percentage of female conductors, viz., 16.10, which cannot possibly exist side by side with the low values for colour blind men and women. The percentages 3.94 and 0.33 cannot, therefore, co-exist in the long run, they cannot correspond.

On the other hand, the relative proportion between colour blind men and women, as given in the old statistics, viz. 1 : 10 or a little more, allow the conclusion, that colour blindness actually occurred to the same extent at that time, as it does now. The proportion 1:10 can exist exactly, only for frequency corresponding to 1 per cent. of colour blind women, 10 per cent. of men, and 18 per cent. of conductors, and when the proportion at that time (1870-80), was about one to ten, the actual values for colour blind men and women must have been just about 10 per cent. and 1 per cent.

Among the possible corresponding values, i.e., values dependent on the condition, that the percentages shall remain constant, and which in their turn are a condition for such constancy, the following might be mentioned:

<table>
<thead>
<tr>
<th>% p.e. colour bl. men demand</th>
<th>7.68 p.c. conductors and 0.16 p.c. colour bl. women (proportion 1 : 25)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>16.38</td>
</tr>
<tr>
<td>10</td>
<td>18.00</td>
</tr>
<tr>
<td>10.07</td>
<td>18.12</td>
</tr>
<tr>
<td>11</td>
<td>19.35</td>
</tr>
<tr>
<td>20</td>
<td>32</td>
</tr>
</tbody>
</table>

This proves that the proportion actually found during research work in colour blindness may be employed as a control for the correctness of the values found, as strikingly seen in this case.

**LITERATURE**

DR. EDRIDGE-GREEN'S THEORIES OF VISION


(To be continued.)

DR. EDRIDGE-GREEN'S THEORIES OF VISION

(continued)

BY

J. HERBERT PARSONS,

LONDON.

III.—COLOUR NAMES

Dr. Edridge-Green divides the spectrum into "psycho-physical units." Thus, the normal person sees six colours—red, orange, yellow, green, blue and violet. Only a few persons see an additional