PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY A
MATHEMATICAL, PHYSICAL & ENGINEERING SCIENCES

Mathematical Contributions to the Theory of Evolution. VIII. On the Inheritance of Characters not Capable of Exact Quantitative Measurement. Part I. Introductory. Part II. On the Inheritance of Coat-Colour in Horses. Part III. On the Inheritance of Eye-Colour in Man

Karl Pearson and Alice Lee

Phil. Trans. R. Soc. Lond. A 1900 **195**, 79-150
doi: 10.1098/rsta.1900.0024

III. *Mathematical Contributions to the Theory of Evolution.—VIII. On the Inheritance of Characters not capable of Exact Quantitative Measurement.*—Part I. *Introductory.* Part II. *On the Inheritance of Coat-colour in Horses.* Part III. *On the Inheritance of Eye-colour in Man.*

By KARL PEARSON, *F.R.S., with the assistance of* ALICE LEE, *D.Sc., University College, London.*

Received August 5,—Read November 16, 1899; withdrawn, rewritten, and again received March 5, 1900.

CONTENTS.

PART I.—*Introductory.*

PART II.—*On Coat-colour Inheritance in the Thoroughbred Horse.*

PART III.—*On Eye-colour Inheritance in Man.*

NOTE.

This memoir was originally presented to the Society on August 5, 1899, and read on November 16, 1899. In working out by the same theory the coefficients of inheritance for Basset Hounds, Mr. LESLIE BRAMLEY-MOORE discovered that the method adopted was not exact enough in its process of proportioning. Accordingly, with the assistance of Mr. L. N. G. FILON, we immensely developed the theory, so that it was necessary to rewrite the theoretical part of the original memoir. This has been carried out in Part VII. of this series. The present memoir consists substantially of the portions of the original memoir relating to the inheritance of coat-colour in Horses and eye-colour in Man, with the numerical details and the resulting conclusions modified, so far as the extended theory rendered this necessary. In the very laborious work of reconstructing my original tables I have received the greatest possible assistance from Dr. ALICE LEE, and I now wish to associate her name with mine on the memoir.* The memoir was at my request returned to me for revision after it had been accepted for the 'Philosophical Transactions.'

PART I.—INTRODUCTORY.

(1.) A CERTAIN number of characters in living forms are capable of easy observation, and thus are in themselves suitable for observation, but they do not admit of an exact quantitative measurement, or only admit of this with very great labour. The object of the present paper is to illustrate a method by which the correlation of such characters may be effectively dealt with in a considerable number of cases. The conditions requisite are the following :—

(i.) The characters should admit of a quantitative order, although it may be impossible to give a numerical value to the character in any individual.

Thus it is impossible at present to give a quantitative value to a brown, a bay, or a roan horse, but it is not impossible to put them in order of relative darkness of shade. Or, again, we see that a blue eye is lighter than a hazel one, although we cannot *à priori* determine their relative positions numerically on a quantitative scale.

Even in the markings on the wings of butterflies or moths, where it might be indefinitely laborious to count the scales, some half dozen or dozen specimens may be taken to fix a quantitative order, and all other specimens may be grouped by inspection in the intervals so determined.

We can even go a stage further and group men or beasts into simply two categories—light and dark, tall and short, dolichocephalic and brachycephalic—and so we might ascertain by the method adopted whether there is, for example, correlation between complexion and stature, or stature and cephalic index.

(ii.) We assume that the characters are a function of some variable, which, if we

---

* I have further to thank Mr. LESLIE BRAMLEY-MOORE, Mr. L. N. G. FILON, M.A., Mr. W. R. MACDONELL, M.A., LL.D. and Miss C. D. FAWCETT, B.Sc., for much help in the arithmetic, often for laborious calculations by processes and on tables, which were none the less of service if they were afterwards discarded for others. To Mr. BRAMLEY-MOORE I owe the extraction and part of the arithmetical reduction of the horse-colour tables.

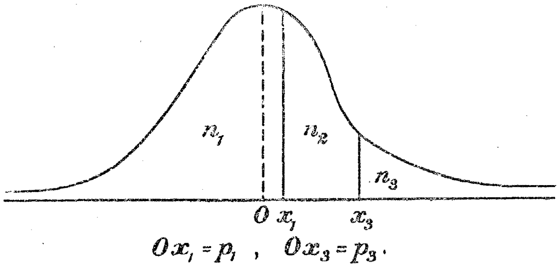
could determine a quantitative scale, would give a distribution obeying—at any rate to a first approximation—the normal law of frequency.

The whole of the theoretical investigations are given in a separate memoir, in which the method applied is illustrated by numerical examples taken from inheritance of eye-colour in man, of coat-colour in horses and dogs, and from other fields. We shall not therefore in this paper consider the processes involved, but we may make one or two remarks on the justification for their use. If we take a problem like that of coat-colour in horses, it is by no means difficult to construct an order of intensity of shade. The variable on which it depends may be the amount of a certain pigment in the hair, or the relative amounts of two pigments. Much the same applies to eye-colour. In both cases we may fail to obtain a true quantitative scale, but we may reasonably argue that, if we could find the quantity of pigment, we should be able to form a continuous curve of frequency. We make the assumption that this curve—to at any rate a first approximation—is a normal curve. Now if we take any line parallel to the axis of frequency and dividing the curve, we divide the total frequency into two classes, which, so long as there is a quantitative order of tint or colour, will have their relative frequency unchanged, however we, in our ignorance of the fundamental variable, distort its scale. For example, if we classify horses into bay and darker, chestnut and lighter, we have a division which is quite independent of the quantitative range we may give to black, brown, bay, chestnut, roan, grey, &c.

Precisely the same thing occurs with eye-colour; we classify into brown and darker, hazel and lighter, and the numbers in these classes will not change with the quantitative scale ultimately given to the various eye-tints. Our problem thus reduces to the following one: Given two classes of one variable, and two classes of a second variable correlated with it, deduce the value of the correlation. Classify sire and foal into bay and darker, chestnut and lighter; mother and daughter into brown and darker, hazel and lighter, and then find the correlation due to inheritance between the coat-colour or eye-colour of these pairs of relations. The method of doing this is given in Memoir VII. of this series. Its legitimacy depends on the assumptions (i.) and (ii.) made above, which may I think be looked upon as justifiable approximations to the truth.

Of course the probable error of the method is larger than we find it to be when correlation is determined from the product-moment. Its value varies with the inequality of the frequency in the two classes given by the arbitrary division. It will be least when we make that frequency as nearly equal as possible—a result which can often be approximately reached by a proper classification. In our present data the probable errors vary from about ·02 to ·04, values which by no means hinder us from drawing general conclusions, and which allow of quite satisfactory general results.

(2.) So far we have only spoken of the two classes, which are necessary if we merely want to determine the correlation. But if we wish to deal with relative variability we must have more than two classes. We have, in fact, in our tables preserved Mr. GALTON's eight eye-colour classes and the seventeen classes under which the coat-colour of thoroughbred horses is classified in WETHERBY's studbooks. Such a classification enables us at any rate approximately to ascertain relative variability, and, what is more, to reconstruct approximately the quantitative scale according to which the tints must be distributed in order that the frequency should be normal. For, in order to attain this result, we have to ascertain from a table of the areas of the normal curve the ratio of the length of the abscissa to the standard deviation which corresponds to any given increase of frequency. Let us suppose that three classes have been made—n_1, n_2, n_3, represented by the areas of the normal curve in the accompanying diagram so marked. Let p_1 and p_3 be the distances of the mean from the two boundaries of n_2. Here p_1 may be negative, or p_3 infinite, &c. Then if $h_1 = p_1/\sigma$, $h_3 = p_3/\sigma$, we find at once, if N = total frequency,



$$\frac{n_1 - n_2 - n_3}{\mathrm{N}} = \sqrt{\frac{2}{\pi}} \int_0^{h_1} e^{-\frac{1}{2}x^2} dx \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{i.}).$$

$$\frac{n_1 + n_2 - n_3}{\mathrm{N}} = \sqrt{\frac{2}{\pi}} \int_0^{h_3} e^{-\frac{1}{2}x^2} dx \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{ii.}).$$

Now the integrals on the right are tabulated, and thus, since the left-hand side is a known numerical quantity, it follows that p_1/σ and p_3/σ, and accordingly the range $(p_3 - p_1)/\sigma$ of the class in terms of the standard deviation, are fully determined.

Thus, if ϵ be the range on the scale of tint or colour of the group of which the observed frequency is n_2, we have $\epsilon = p_3 - p_1$, and thus $\epsilon/\sigma = q$ say, is known. For a second series $\epsilon/\sigma' = q'$. Hence $\sigma/\sigma' = q'/q$, and accordingly the ratio of the variabilities of the two series is determined.

Again, the ratio $p_1/(p_3 - p_1)$ enables us to find the position of the mean in terms of the range on the scale occupied by the tint corresponding to the frequency n_2. As a rule we shall take this tint to be that in which the mean actually lies, in which case we shall have $p_1/(p_3 + p_1)$ as determining the ratio in which the mean divides the true quantitative range of this particular tint.

(3.) Let

$$\eta = p_1 (p_3 - p_1) = h_1/(h_3 - h_1) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{iii.}),$$

$$\zeta = \sigma/\sigma' = (h_3' - h_1')/(h_3 - h_1) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{iv.}).$$

It remains to find the probable errors of these quantities.

Suppose Σ_x to be the standard deviation for the errors in a quantity x, and R_{xy} the correlation coefficient for errors in two quantities x and y.

Further let

$$H = \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2}h^2} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{v.}),$$

where subscripts and dashes may be attached to H to correspond to like distinguishing marks attached to h.

Since

$$\frac{2n_1 - N}{2N} = \frac{1}{\sqrt{2\pi}} \int_0^{h_1} e^{-\frac{1}{2}x^2} dx \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{vi.}),$$

we have at once $\delta n_1 = NH_1 \delta h_1$,

and $\Sigma_{h_1} = \Sigma_{n_1}/(NH_1)$ . . . . (vii.).

Similarly, $\delta n_3 = - NH_3 \delta h_3$, whence:

$$\Sigma_{h_3} = \Sigma_{n_3}/(NH_3) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{viii.}).$$

Further, we have $\Sigma_{h_1}\Sigma_{h_3}R_{h_1h_3} = - \Sigma_{n_1}\Sigma_{n_3}R_{n_1n_3}/(N^2H_1H_3)$ . . . . . (ix.);

but, as is shewn in Part VII., § 4,

$$\Sigma_{n_1}{}^2 = \frac{n_1(N - n_1)}{N}, \qquad \Sigma_{n_3}{}^2 = \frac{n_3(N - n_3)}{N} \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{x.}),$$

$$\Sigma_{n_1}\Sigma_{n_3}R_{n_1n_3} = - \frac{n_1n_3}{N} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{xi.}).$$

Thus we find

$$\text{Probable error of } h_1 = \cdot 67449 \Sigma_{h_1}$$

$$= \frac{\cdot 67449}{\sqrt{N}} \frac{1}{H_1} \sqrt{\frac{n_1(N - n_1)}{N^2}} \quad . \quad . \quad . \quad . \quad . \quad (\text{xii.}).$$

$$\text{Probable error of } h_3 = \frac{\cdot 67449}{\sqrt{N}} \frac{1}{H_3} \sqrt{\frac{n_3(N - n_3)}{N^2}} \quad . \quad . \quad . \quad . \quad . \quad (\text{xiii.}).$$

Correlation in errors in h_1 and h_3, or $R_{h_1h_3}$, is given by

$$\Sigma_{h_1}\Sigma_{h_3}R_{h_1h_3} = \frac{n_1n_3}{N^3H_1H_3} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{xiv.}).$$

Let $u = h_3 - h_1$, $u' = h_3{}' - h_1{}'$ be the ratio to the respective standard deviations of the ranges corresponding to the groups n_2 and $n_2{}'$. Then

$$\Sigma_u{}^2 = \Sigma_{h_1}{}^2 + \Sigma_{h_3}{}^2 - 2\Sigma_{h_1}\Sigma_{h_3}R_{h_1h_3}$$

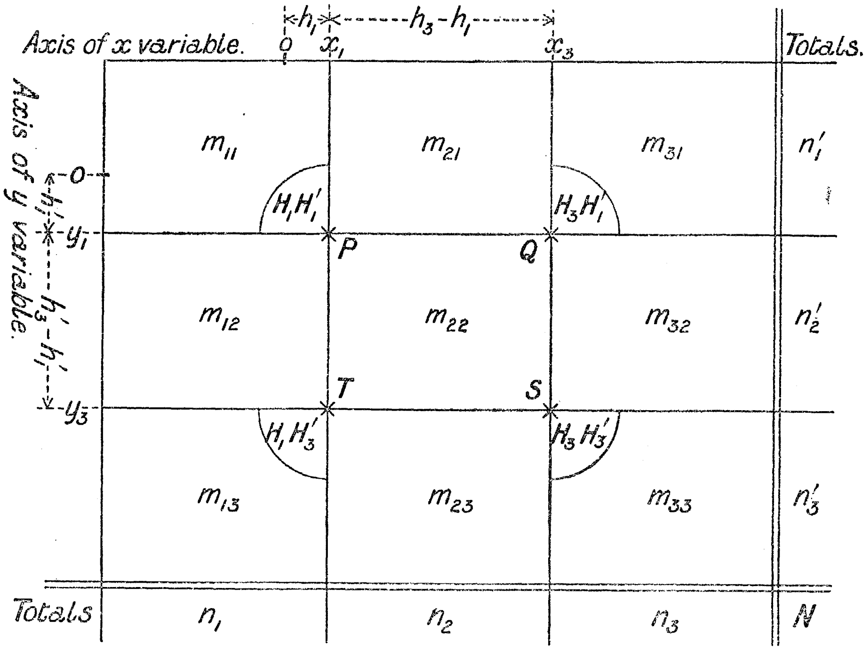
$$= \frac{1}{N^3}\left\{\frac{n_1(N - n_1)}{H_1{}^2} + \frac{n_3(N - n_3)}{H_3{}^2} - \frac{2n_1n_3}{H_1H_3}\right\};$$

whence, if ν be a proportional frequency $= n/N$, we readily find

$$\text{Probable error of } u = \frac{\cdot 67449}{\sqrt{N}} \left\{\frac{\nu_1}{H_1{}^2} + \frac{\nu_3}{H_3{}^2} - \left(\frac{\nu_1}{H_1} + \frac{\nu_3}{H_3}\right)^2\right\}^{\frac{1}{2}} \quad . \quad . \quad . \quad (\text{xv.}).$$

$$\text{Probable error of } u' = \frac{\cdot 67449}{\sqrt{N}} \left\{\frac{\nu_1{}'}{H_1{}'^2} + \frac{\nu_3{}'}{H_3{}'^2} - \left(\frac{\nu_1{}'}{H_1{}'} + \frac{\nu_3{}'}{H_3{}'}\right)^2\right\}^{\frac{1}{2}} . \quad . \quad . \quad (\text{xvi.}).$$

I now proceed to determine the correlation in the errors made in determining the ranges corresponding to any two classes of any two variables which are correlated. For this purpose let the frequency correlation table be dressed as follows, in the diagram below.



Here m_{ij} denotes the frequency of individuals common to the two classes n_i and n'_j. Let M_{ij} denote its "conjugate," or all the frequency which appears in neither n_i nor n'_j; then

$$N = M_{ij} + n_i + n'_j - m_{ij} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (xvii.).$$

As before, we have

$$\Sigma_{n_i}^{\ 2} = \frac{n_i(N - n_i)}{N}, \qquad \Sigma_{n'_j}^{\ 2} = \frac{n'_j(N - n'_j)}{N} \quad . \quad . \quad . \quad . \quad (xviii.).$$

$$\Sigma_{M_{ij}}^{\ 2} = \frac{M_{ij}(N - M_{ij})}{N}, \qquad \Sigma_{m_{ij}}^{\ 2} = \frac{m_{ij}(N - m_{ij})}{N} \quad . \quad . \quad . \quad . \quad (xix.).$$

Further, since m_{ij} and M_{ij} are mutually exclusive, we have

$$\Sigma_{M_{ij}}\Sigma_{m_{ij}}R_{M_{ij}m_{ij}} = -\frac{M_{ij}m_{ij}}{N} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (xx.).$$

From (xvii.) we have for small variations

$$\delta n_i + \delta n'_j = \delta m_{ij} - \delta M_{ij}.$$

Hence

$$2\Sigma_{n_i}\Sigma_{n'_j}R_{n_i n'_j} = \Sigma_{m_{ij}}^{\ 2} + \Sigma_{M_{ij}}^{\ 2} - \Sigma_{n_i}^{\ 2} - \Sigma_{n_{ij}}^{\ 2} - 2\Sigma_{m_{ij}}\Sigma_{M_{ij}}R_{M_{ij}m_{ij}} \quad . \quad . \quad . \quad (xxi).$$

Substituting the values given above we find, after some reductions,

$$\Sigma_{n_i}\Sigma_{n'_j}\mathrm{R}_{n_i n'_j} = \frac{\mathrm{N}m_{ij} - n_i n'_j}{\mathrm{N}} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(xxii.)}$$

This result, which is extremely simple in form, gives the correlation in errors made in determining the frequencies in any two classes whatever of any two correlated variables.

I next proceed to find the correlation between errors in u and u', the ratio of the ranges occupied by any two classes to their respective standard deviations.

We have

$$\delta n_2 + \delta n_3 = -\mathrm{NH}_1\delta h_1\,;$$
$$\delta n_3 = -\mathrm{NH}_3\delta h_3.$$

Hence $$\delta(h_3 - h_1) = \frac{\delta n_2}{\mathrm{NH}_1} + \frac{\delta n_3}{\mathrm{N}}\left(\frac{1}{\mathrm{H}_1} - \frac{1}{\mathrm{H}_3}\right).$$

Similarly $$\delta(h_3' - h_1') = \frac{\delta n'_2}{\mathrm{NH}_1'} + \frac{\delta n_3'}{\mathrm{N}}\left(\frac{1}{\mathrm{H}_1'} - \frac{1}{\mathrm{H}_3'}\right).$$

Multiply the first by the second, and summing as usual for all possible errors, we have, by using (xxii.)

$$\Sigma_u\Sigma_{u'}\mathrm{R}_{uu'} = \frac{1}{\mathrm{N}}\left\{\frac{\mathrm{N}m_{22} - n_2 n_2'}{\mathrm{N}^2\mathrm{H}_1\mathrm{H}_1'} + \frac{\mathrm{N}m_{23} - n_2 n_3'}{\mathrm{N}^2\mathrm{H}_1}\left(\frac{1}{\mathrm{H}_1'} - \frac{1}{\mathrm{H}_3'}\right) + \frac{\mathrm{N}m_{32} - n_2' n_3}{\mathrm{N}^2\mathrm{H}_1'}\left(\frac{1}{\mathrm{H}_1} - \frac{1}{\mathrm{H}_3}\right)\right.$$
$$\left. + \left(\frac{\mathrm{N}m_{33} - n_3 n_3'}{\mathrm{N}^2}\right)\left(\frac{1}{\mathrm{H}_1} - \frac{1}{\mathrm{H}_3}\right)\left(\frac{1}{\mathrm{H}_1'} - \frac{1}{\mathrm{H}_3'}\right)\right\}.$$

Collecting the like H's we find, after very considerable reductions,

$$\Sigma_u\Sigma_{u'}\mathrm{R}_{uu'} = \frac{1}{\mathrm{N}}\left\{\frac{\mathrm{N}m_{11} - n_1 n_1'}{\mathrm{N}^2\mathrm{H}_1\mathrm{H}_1'} + \frac{\mathrm{N}m_{33} - n_3 n_3'}{\mathrm{N}^2\mathrm{H}_3\mathrm{H}_3'} + \frac{\mathrm{N}m_{13} - n_1 n_3'}{\mathrm{N}^2\mathrm{H}_1\mathrm{H}_3'} + \frac{\mathrm{N}m_{31} - n_3 n_1'}{\mathrm{N}^2\mathrm{H}_3\mathrm{H}_1'}\right\}$$
$$. \quad . \quad . \quad . \quad \text{(xxiii.)},$$

or, $$\Sigma_u\Sigma_{u'}\mathrm{R}_{uu'} = \frac{1}{\mathrm{N}}\left\{\frac{\mu_{11} - \nu_1\nu_1'}{\mathrm{H}_1\mathrm{H}_1'} + \frac{\mu_{33} - \nu_3\nu_3'}{\mathrm{H}_3\mathrm{H}_3'} + \frac{\mu_{13} - \nu_1\nu_3'}{\mathrm{H}_1\mathrm{H}_3'} + \frac{\mu_{31} - \nu_3\nu_1'}{\mathrm{H}_3\mathrm{H}_1'}\right\} \quad . \quad . \quad \text{(xxiii.}^{\text{bis}}\text{)}.$$

where $\mu_{ij} = m_{ij}/\mathrm{N}$ = proportional frequency.

A glance at our diagram on the previous page of the correlation table divided into nine classes, shows at once the symmetrical formation of this result. By writing at the points P, Q, S, and T, the ordinate there of the normal surface, on the supposition of no correlation and N = 1, the construction of the result is still more clearly brought out.

We are now in a position to determine the probable errors of η and ζ. We have

$$\delta\eta = \frac{h_3\delta h_1 - h_1\delta h_3}{u^2}.$$

Hence

$$\Sigma_\eta^2 = \frac{1}{u^4}\left(h_3{}^2\Sigma_{h_1}{}^2 + h_1{}^2\Sigma_{h_3}{}^2 - 2h_3h_1\Sigma_{h_1}\Sigma_{h_3}\mathrm{R}_{h_1h_3}\right)$$

$$= \frac{h_1{}^2h_3{}^2}{u^4\mathrm{N}}\left\{\frac{n_1(\mathrm{N}-n_1)}{(h_1\mathrm{H}_1)^2\,\mathrm{N}^2} + \frac{n_3(\mathrm{N}-n_3)}{(h_3\mathrm{H}_3)^2\mathrm{N}^2} - \frac{2n_1n_3}{(h_1\mathrm{H}_1)(h_2\mathrm{H}_3)\mathrm{N}^2}\right\}.$$

Or, Probable error of η

$$= \frac{\cdot 67449}{\sqrt{\mathrm{N}}}\,\frac{h_1h_3}{u^2}\left\{\frac{\nu_1}{(h_1\mathrm{H}_1)^2} + \frac{\nu_3}{(h_3\mathrm{H}_3)^2} - \left(\frac{\nu_1}{h_1\mathrm{H}_1} + \frac{\nu_3}{h_3\mathrm{H}_3}\right)^2\right\}^{\frac{1}{2}} \quad . \quad . \quad . \quad \text{(xxiv.)}.$$

where u is the range $h_3 - h_1$, and ν_1 and ν_3 are the proportional frequencies, as before. Care must be taken, if the class n_2 cover, as it usually will in our present investigations, the mean, to put h_1 negative within the radical. In other words, for a class covering the mean we have

Probable error of η

$$= \frac{\cdot 67449}{\sqrt{\mathrm{N}}}\,\frac{h_1h_3}{(h_1+h_3)^2}\left\{\frac{\nu_1}{(h_1\mathrm{H}_1)^2} + \frac{\nu_3}{(h_3\mathrm{H}_3)^2} - \left(\frac{\nu_1}{h_1\mathrm{H}_1} - \frac{\nu_3}{h_3\mathrm{H}_3}\right)^2\right\}^{\frac{1}{2}} \quad . \quad . \quad \text{(xxv.)}.$$

Lastly we have

$$\zeta = u'/u\,,$$

or,

$$\delta\zeta = \frac{u\delta u' - u'\delta u}{u^2} = \frac{u'}{u}\left(\frac{\delta u'}{u'} - \frac{\delta u}{u}\right).$$

Hence

$$\Sigma_\zeta{}^2 = \frac{u'^2}{u^2}\left\{\frac{\Sigma_{u'}{}^2}{u'^2} + \frac{\Sigma_u{}^2}{u^2} - \frac{2\Sigma_u\Sigma_u\mathrm{R}_{uu'}}{uu'}\right\}.$$

Thus : Probable error of ζ

$$= \cdot 67449\zeta\left\{\frac{\Sigma_u{}^2}{u^2} + \frac{\Sigma_{u'}{}^2}{u'^2} - \frac{2\Sigma_u\Sigma_{u'}\mathrm{R}_{uu'}}{uu'}\right]^{\frac{1}{2}} \quad . \quad . \quad . \quad . \quad . \quad \text{(xxvi.)},$$

where we have by (xv.), (xvi.), and (xxiii.$^{\text{bis}}$)

$$\Sigma_u{}^2 = \frac{1}{\mathrm{N}}\left\{\frac{\nu_1}{\mathrm{H}_1{}^2} + \frac{\nu_3}{\mathrm{H}_3{}^2} - \left(\frac{\nu_1}{\mathrm{H}_1} + \frac{\nu_3}{\mathrm{H}_3}\right)^2\right\},$$

$$\Sigma_{u'}{}^2 = \frac{1}{\mathrm{N}}\left\{\frac{\nu_1'}{\mathrm{H}_1'^2} + \frac{\nu_3'}{\mathrm{H}_3'^2} - \left(\frac{\nu_1'}{\mathrm{H}_1'} + \frac{\nu_3'}{\mathrm{H}_3'}\right)^2\right\},$$

$$\Sigma_u\Sigma_{u'}\mathrm{R}_{uu} = \frac{1}{\mathrm{N}}\left\{\frac{\mu_{11} - \nu_1\nu_1'}{\mathrm{H}_1\mathrm{H}_1'} + \frac{\mu_{33} - \nu_3\nu_3'}{\mathrm{H}_3\mathrm{H}_3'} + \frac{\mu_{13} - \nu_1\nu_3'}{\mathrm{H}_1\mathrm{H}_3'} + \frac{\mu_{31} - \nu_3\nu_1'}{\mathrm{H}_3\mathrm{H}_1'}\right\},$$

where, as before, μ's and ν's represent proportional frequencies.

In the following investigations on coat-colour and eye-colour inheritance I have not thought it needful to give in every one of the thirty-six relationships dealt with the probable errors of the means, ratio of variabilities, and the coefficients of inheritance (η, ζ, and r). The arithmetical labour would have been too great, for the expressions as given above are somewhat complex. It is, however, necessary to keep the approximate values of these probable errors in view, and, as our results classify themselves easily into groups for which our data, as well as the intensity of heredity, are approximately the same, one series of these errors has been found for each group.

(4.) If we have ground for our assumption that the variable at the basis of our tint classification can be so selected as to give a normal distribution, we may determine the relative lengths on the scale of that variable occupied by each tint or shade.

Thus if σ_1 be the standard deviation of the variable for male eye-colour, σ_2 for female eye-colour, I measured the range on the scale in terms of σ_1 and σ_2 for Mr. GALTON'S eight eye-colour tints for 3000 cases of male and 3000 cases of female eye-colour. I found the spaces occupied on the unknown scale to be as follows :—

No.	Tint.	Range in terms of σ_2.	Range in terms of σ_1.
1	Light blue	∞	∞
2	Blue, dark blue . . .	1·39276	1·34918
3	Grey, blue-green . . .	·73468	·77596
4	Dark grey, hazel . . .	·40027	·41992
5	Light brown	·03893	·00856
6	Brown	·43679	·35895
7	Dark brown.	·84161	·64167
8	Very dark brown, black.	∞	∞

These results are not so regular as we might have hoped for, on the assumption that the ratio of σ_1/σ_2 would be the same from whatever part of the scale it be determined. The general conclusion, however, would be that σ_1 is slightly larger than σ_2, which is confirmed by other investigations. Actually a tint may be rather vaguely described, and where the data were obtained by untrained observers without the assistance of a plate of eye-colours, a good deal of rather rough classification is likely to have taken place. I do not think it would be safe to go further than stating that on the quantitative colour scale the tints as described must occupy spaces in about the following proportions :—

Light Blue.	Blue, Dark Blue.	Grey, Blue-Green.	Dark Grey, Hazel.	Light Brown.	Brown.	Dark Brown.	Very dark Brown, Black.
∞	1·37	·75	·41	·02	·40	·74	∞

Taking 2000 colts and 2000 fillies, the standard deviations being σ_1 and σ_2 respectively, I have worked out the coat-colour ranges in terms of σ_2 and σ_1 for each of the sixteen colours* occurring in the records. We have the following results :—

---

* See p. 92, below.

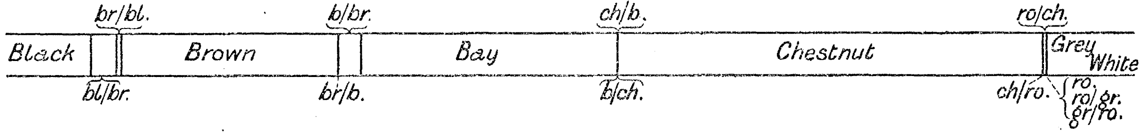
Tint.	Range in σ_2.	Range in σ_1.		Range in σ_2.	Range in σ_1.
1	∞	∞	9	·00000	·00000
2	·12683	·10768	10	1·96956	2·01658
3	·00000	·03313	11	·00000	·00000
4	·91747	1·11055	12	·02490	·00000
5	·00000	·00352	13	·00000	·00000
6	·11059	·10451	14	·00000	·00000
7	1·34684	1·27688	15	·00000	·00000
8	·00000	·00000	16	∞	∞

Here again it seems to me that the most we can safely do is to consider that on a suitable scale the relative lengths occupied by the classes of coat-colours recognised by thoroughbred horse breeders would be somewhat as follows :—

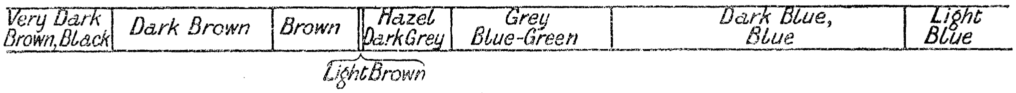
bl.	bl./br.	br./bl.	br.	br./b.	b./br.	b.	b./ch.	ch./b.	ch.	ch./ro.	ro./ch.	ro.	ro /gr.	gr /ro.	gr.
∞	·12	·02	1·01	·00	·11	1·31	·00	·00	1·99	·00	·01	·00	·00	·00	∞

The reader must carefully bear in mind that these represent scale-lengths occupied by the coat-colour and not the frequency of horses of these individual coat-colours. What we are to understand is this: that if eye-colour in man and coat-colour in horses were measured on such quantitative scales as we have given in skeleton, then the distribution of the frequency of the several colours would be very approximately normal. The actual skeleton scales are represented in the accompanying diagram, which puts them at once before the eye.

Normal Scale of Colour Ranges in Thoroughbred Horses.



Normal Scale of Eye Colour Ranges in Man.



(5.) It is necessary here to draw attention to a distinction of some importance in heredity, namely, that between *blended* and *exclusive* inheritance. In my treatment of the law of ancestral heredity,* it is assumed that we have to deal with a quantitatively measurable character, and that the ancestry contribute to the quantity of this character in certain proportions which on the average are fixed and follow certain definite numerical laws. Such an inheritance is *blended* inheritance. But another

---

* 'Roy. Soc. Proc.,' vol. 62, p. 386.

type of inheritance is possible. We may have one progenitor, prepotent over all others and absorbing all their shares, who hands down to the offspring not a proportion of his character, but the whole of it without blend. If this progenitor is a parent we have *exclusive* inheritance, if a higher ancestor a case of reversion. I have dealt at some length with this type of inheritance under the title of the Law of Reversion in another paper.* We must consider in outline the main features of such inheritance, for the cases of eye-colour in man and coat-colour in the horse approximate more closely to the numerical values required by it, than to those indicated by the law of ancestral heredity. The chief feature of exclusive inheritance is the absolute prepotency of one parent with regard to some organ or character. It need not always be the parent of the same sex, or the same parent throughout the same family. Some offspring may take absolutely after one, others after another parent for this or that organ or character only. I believe Mr. GALTON first drew attention, in his 'Natural Inheritance' (p. 139), to this exclusive or, as he terms it, *alternative* heritage in eye-colour. In going through his data again I have been extremely impressed by it; even those cases in which children might be described as a blend, rare as they are, are quite possibly the result of reversion rather than blending. If we suppose exclusive inheritance to be absolute, and there to be no blending or reversion, it is not hard to determine the laws of inheritance. Supposing the population stable, one-half the offspring of parentages with one parent of given eye-colour would be identical with that parent in eye-colour, the other half would regress to the general population mean, *i.e.*, the mean eye-colour of all parents. Hence, taken as a whole, the regression of children on the parent would be ·5. In the case of the grandparent the regression would be ·25; of a great grandparent ·125, and so on. With an uncle a quarter of the offspring of his brother will be identical in eye-colour with him, the other three-quarters will regress to the population mean, thus the regression will be ·25. If we have n brethren in a family, and take all possible pairs of fraternal relations out of it, there will be $\frac{1}{2}n(n-1)$ such pairs; $\frac{1}{2}n$ brothers will have the same eye-colour that of one parent, the other $\frac{1}{2}n$ brother that of the other parent. Hence selecting any one brother, $\frac{1}{2}n - 1$ would have his eye-colour, and on the average $\frac{1}{2}n$ would have regressed to the mean of the general population. In other words, the coefficient of regression would be $(\frac{1}{2}n - 1)/(\frac{1}{2}n - 1 + \frac{1}{2}n) = (\frac{1}{2}n - 1)/(n - 1)$.

Accordingly $n = 3$ Regression $= ·25$
$n = 4$,, $= ·3333$
$n = 4·7$,, $= ·3649$
$n = 5$,, $= ·375$
$n = 5·3$,, $= ·3833$
$n = 6$,, $= ·4$
$n = \infty$,, $= ·5$

---

* 'Roy. Soc. Proc.,' vol. 66, pp. 140 *et seq.*

It will at first appear, therefore, that the fraternal regression with the size of families actually occurring will vary from ·35 to ·4.

To some extent these values would be modified by assortative mating, which actually exists in the case of eye-colour. The correlations between parent and offspring and between brothers would both be slightly increased. Thus if ρ be the coefficient of assortative mating, R_f the fraternal correlation with and r_f without assortative mating, and r the coefficient for parent and offspring,*

$$R_f = \frac{r_f + 2\rho r^2}{1 - 2\rho r^2}.$$

If we put $r_f = ·36$, $r = ·5$, $\rho = ·1$, we find

$$R_f = ·39.$$

Thus we see that the regression or correlation for fraternal inheritance in the case of exclusive inheritance could not, with the average size of families, be very far from ·4 of blended inheritance.

A further source which can modify immensely, however, the fraternal correlation is the prepotency of one or other parent, not universally, but within the individual family. In the extreme case all the offspring might be alike in each individual family. Thus fraternal correlation might be perfect although parental correlation were no greater than ·5. Hence, where for small families we get a fraternal correlation greater than ·4 to ·5, it is highly probable that there exists either a sex prepotency (in this case, one of the parental correlations will be considerably greater than the other) or an individual prepotency (in which case the parental correlations based on the average may be equal). We shall see that fraternal correlations occur greater than ·5 in our present investigations. I have dealt with these points in my Memoir on the 'Law of Reversion,'† and also in the second edition of the 'Grammar of Science.'‡

Another point also deserves notice, namely, that with the series ·5, ·25, ·125, &c., for the ancestral coefficients in the direct line, the theorems proved in my Memoir on Regression, Heredity, and Panmixia§ for the series of coefficients $r, r^2, r^3 \ldots$ exactly hold. That is to say, if we have absolutely exclusive inheritance, the partial regression coefficients for direct ancestry are all zero except in the case of the parents. This it will be observed is not in agreement with Mr. GALTON'S views as expressed in Chapter VIII. of the 'Natural Inheritance.' But I do not see how it is possible to treat exclusive inheritance on the hypothesis that the parental regression is about ·3.‖ Actual investigation shows that for this very character, *i.e.*, eye-colour, it is nearer ·5. If we take Table XIX. of Mr. GALTON'S appendix, and make the following groups, both

---

* This is shown in a paper not yet published on the influence of selection on correlation.

† 'Roy. Soc. Proc.,' vol. 66, pp. 140 *et seq.*.

‡ "On Prepotency," p. 459; "On Exclusive Inheritance," p. 486.

§ 'Phil. Trans.,' A, vol. 187, p. 302, etc.

‖ Mr. GALTON takes $\frac{1}{3}$ throughout his arithmetic.

parents light, one parent light and one medium, one light and one dark, we reach the following results :—

Parents' eye-colour.	Children, actual.		Light-eyed children, calculated.	
	Total.	Light-eyed.	Exclusive inheritance.	Ancestral law with knowledge of parents and grandparents.
Both light	355	334	355	321
Light and medium .	215	170	161	160
Light and dark . .	211	107	105	117

Here the exclusive inheritance leads us to misplace thirty-two and the ancestral law thirty-three children. The evidence, therefore, of the correctness of the latter is hardly greater than that of the former. Indeed, if the former were modified for reversion, it would very possibly give better results than the latter.

I am inclined accordingly to look upon eye-colour inheritance as an exclusive inheritance modified by reversion, and, to some extent, by assortative mating, rather than a mixture of exclusive inheritance with a slight amount of blending. In either case exclusive inheritance gives results like the above so closely in accord with the ancestral law that the latter might be supposed to hold. But, theoretically, I do not understand how the ancestral law is compatible with exclusive inheritance. Theoretically, we have values of parental, avuncular, and grand-parental correlation greater than the ancestral law would permit of, and these theoretical values are, on the whole, closer to observation, as we shall see in the sequel, than those given by the law of ancestral heredity. The following table gives the two systems :—

TABLE I.—Theoretical Values of the Regression Coefficients.

Relationship.	Blended inheritance, ancestral law.	Exclusive inheritance, absolute, no reversion.
Parent and offspring	·3	·5
Grandparent and offspring . . .	·15	·25
Great-grandparent and offspring .	·075	·125
Brethren	·4	·35 to ·5*
Uncle and nephew	·15	·25

Now, if exclusive inheritance be modified by reversion or assortative mating, or if blended inheritance be modified by "taxation,"† then we shall get values different

---

* This varies with the size of the family.

† 'Roy. Soc. Proc.,' vol. 62, p. 402.

from the above, and possibly filling up the numerical gap between them. To this point I shall return when dealing with the observed values for eye-colour in man.

PART II.—ON COLOUR-INHERITANCE IN THOROUGHBRED RACEHORSES.

(6.) All the data were extracted from WEATHERBY'S stud-books, the colours being those of the horses as yearlings. My first step was to form an order, not a quantitative scale, of horse-colours. With this end in view, the recorded colours were examined, and, including the arabs, the following seventeen colours were at first found :—

1. Black (bl.).
2. Black or brown (bl./br.).
3. Brown or black (br./bl.).
4. Brown (br.).
5. Brown or bay (br./b.).
6. Bay or brown (b./br.).
7. Bay (b.).
8. Bay or chestnut (b./ch.).
9. Chestnut or bay (ch./b.).
10. Chestnut (ch.).
11. Chestnut or roan (ch./ro.).
12. Roan or chestnut (ro./ch.).
13. Roan (ro.).
14. Roan or grey (ro./g.).
15. Grey or roan (g./ro.).
16. Grey (g.).
17. White (w.).

Now, if we take the alternative colours to mean that the first alternative is the prominent element, we see that these colours in use among breeders admit of *only one arrangement from black to white.* That is to say, that a continuous shade-change is actually in use for the colour-nomenclature of thoroughbred horses.* Thus without any hypothesis as to the quantitative relative values of bay or roan, we have an order which serves for all our present purposes. Following this order, Appendix I., Tables I.—XII., for the colour correlation of related pairs of horses was compiled by Mr. LESLIE BRAMLEY-MOORE from the stud-books. When dealing with relationship in the ♀ line only, no weight has been given to fertility, as each mare has had only one foal attributed to it, or two in the case of fraternal correlation. In the case of the ♂ line, the colours of the older sires were harder to ascertain, and we did not obtain altogether more than 600 sire-colours. Thus one, two, or, in a few cases, three or four colts or fillies were taken from each sire.

I shall now discuss the results which may be drawn from these tables for the theory of heredity, first placing in a single table all the numerical constants calculated from the data in Tables I. to XII. of Appendix I.

---

* Among the 6000–8000 horses dealt with only *four* were found with colours not entered in this scale, but these entries of bl./ch., br./ch., b./ro., in no way contradict the *order* of the scale, but merely show a rougher appreciation on the part of the nomenclator, or possibly printers' or editor's errors.

TABLE II.—Coat-colour Inheritance in Thoroughbred Horses.

Pair of relatives.		Division of bay range by the mean		Ratio of variabilities.		Coefficients of correlation.	Coefficients of regression.		Number of cases.
x.	y.	η_x.	η_y.	$\zeta = \sigma_x/\sigma_y$.	$\zeta = \sigma_y/\sigma_x$.	r_{xy}.	R_{xy}.	R_{yx}.	N.
Sire.	Colt. .	·6111	·5713	·8712	1·1478	·4913	·4280	·5639	1300
Sire.	Filly .	·6061	·5719	·8298	1·2051	·5422	·4499	·6534	1050
Dam	Colt. .	·5359	·6027	·9500	1·0526	·4862	·4619	·5118	1000
Dam	Filly .	·5565	·6051	·9036	1·1067	·5668	·5122	·6273	1000
Maternal grandsire	Colt. .	·6583	·5867	·7030	1·4225	·3590	·2524	·5107	1000
Maternal grandsire	Filly .	·6359	·6042	·7678	1·3024	·3116	·2392	·4058	1000
Colt . . . . . . (Half	Colt. . siblings)	·5908	·5908	1	1	·3551	·3551	·3551	2000
Colt . . . . . (Whole	Colt. . siblings)	·5620	·5620	1	1	·6232	·6232	·6232	2000
Filly . . . . . . (Half	Filly . siblings)	·5665	·5665	1	1	·4265	·4265	·4265	2000
Filly . . . . . . (Whole	Filly . siblings)	·5684	·5684	1	1	·6928	·6928	·6928	2000
Filly . . . . . . (Half	Colt. . siblings)	·5633	·5865	·9607	1·0409	·2834	·2723	·2950	1000
Filly . . . . . . (Whole	Colt. . siblings)	·5410	·5711	·9555	1·0466	·5827	·5568	1·0466	1000

In this table $\mathrm{R}_{xy} = r_{xy}\sigma_x/\sigma_y$, $\mathrm{R}_{yx} = r_{xy}\sigma_y/\sigma_x$. Half-siblings* are those having the same dam, but different sires. Further, η is measured from the brown end of the bay range up to the mean.

(7.) *On the Mean Coat-Colour of Horses.*—If our theory be correct, this colour will not differ much from the median colour, and we notice at once a secular change going on. We have the following order:—

Maternal grandsire of colt . . . . . η = ·6583
Maternal grandsire of filly . . . . . . = ·6359
Sire of colt . . . . = ·6111
Sire of filly . . . . = ·6061
Colt (mean value of seven series) . . . = ·5816

Dam of colts . . . . η = ·5359
Dam of fillies . . . . = ·5565
Fillies (mean value of seven series) . . = ·5753

---

* I have introduced this expression in my paper on "The Law of Reversion," 'Roy. Soc. Proc.,' vol. 66, as a convenient expression for a pair of offspring from same parents whatever be their sex.

Now the colours of all the horses are returned when they are foals, so that there is no question of any variation of colour with age, yet we notice that—

(i.) The horse is lighter in colour than the mare.

(ii.) If we go back two generations (grandsire) the horse is lighter than if we only go back one generation (sire), and the sires are again lighter than their colts. In other words, there seems a progressive change towards a darker coat.

(iii.) On the other hand, the mares one generation back appear to be darker than their daughters.

(iv.) The average sire of colts is lighter than the average sire of fillies; the average dam of colts is darker than the average dam of fillies.

Now these conclusions seem to indicate that the older horse was lighter in coat, and the older mare darker in coat than either the colt or filly of to-day, and that there is a tendency in the thoroughbred racehorse of to-day to approach to an equality of colour in the two sexes, an equality which is a blend of the sensibly divergent sex-colour of the older generation.

Whether this secular change is due to the "breeding out" of the influence of light Arabian sires, or to a tendency in the past to select light-coloured sires and dark-coloured mares for breeding, or to the fact that such coloured sires and mares are the most fertile, *i.e.*, to an indirect effect of reproductive selection, is not so easy to determine. But what does appear certain is that the average thoroughbred is approaching to a blend between its male and female ancestry, which were sensibly divergent.*

(8.) *On the Relative Variability of Sex and Class in Horses.*—The following table gives the length of the bay range in terms of the standard deviation for each class. If ϵ represent this range, then in terms of the previous notation $\epsilon = u \times \sigma = u' \times \sigma'$, and from these values of u and u' the ratio, $\zeta = \sigma/\sigma'$ of Table II. was calculated.

---

* Mean of dams and sires of colts = ·5735, *i.e.*, $\frac{1}{2}$(·6111 + ·5359).
Mean of dams and sires of fillies = ·5813, *i.e.*, $\frac{1}{2}$(·6061 + ·5565).

These are curiously enough almost exactly equal to the mean values ·5753 and ·5816 obtained for fillies and colts. This *inverse* relationship is too close to the probable errors of the quantities under investigation for real stress to be laid on it, but it may still turn out to be suggestive.

III.—Table of Bay Ranges.

Relative Pair.		Bay Range.		Probable Error of Median.	
x.	y.	$u \times \sigma_x$.	$u' \times \sigma_y$.	x.	y.
Sire	Colt	$1{\cdot}46943\sigma_x$	$1{\cdot}28019\sigma_y$	± ·0160	± ·0183
Sire	Filly	$1{\cdot}64075\sigma_x$	$1{\cdot}36149\sigma_y$	± ·0159	± ·0192
Dam	Colt	$1{\cdot}36645\sigma_x$	$1{\cdot}29819\sigma_y$	± ·0196	± ·0206
Dam	Filly	$1{\cdot}38165\sigma_x$	$1{\cdot}24845\sigma_y$	± ·0193	± ·0214
Maternal grandsire	Colt	$1{\cdot}69694\sigma_x$	$1{\cdot}19293\sigma_y$	± ·0158	± ·0224
Maternal grandsire	Filly	$1{\cdot}65021\sigma_x$	$1{\cdot}26702\sigma_y$	± ·0162	± ·0211
Colt (Half	Colt siblings)	$1{\cdot}23953\sigma_x$	$1{\cdot}23953\sigma_y$	± ·0153	± ·0153
Colt (Whole	Colt siblings)	$1{\cdot}27688\sigma_x$	$1{\cdot}27688\sigma_y$	± ·0148	± ·0148
Filly (Half	Filly siblings)	$1{\cdot}39619\sigma_x$	$1{\cdot}39619\sigma_y$	± ·0135	± ·0135
Filly (Whole	Filly siblings)	$1{\cdot}34684\sigma_x$	$1{\cdot}34684\sigma_y$	± ·0140	± ·0140
Filly (Half	Colt siblings)	$1{\cdot}33479\sigma_x$	$1{\cdot}28229\sigma_y$	± ·0202	± ·0208
Filly (Whole	Colt siblings)	$1{\cdot}41501\sigma_x$	$1{\cdot}35207\sigma_y$	± ·0189	± ·0198

To explain the last double column I note that Mr. SHEPPARD has shown (' Phil. Trans.,' A, vol. 192, p. 134) that the probable error of the median equals

$$\cdot 84535\ \sigma/\sqrt{\text{N}}.$$

Hence in terms of the bay range we have

$$\frac{\text{probable error of median}}{\text{length of bay range}} = \cdot 84535/(u\sqrt{\text{N}}).$$

I have found that this simple result gives a value close to but slightly larger than the probable error of the quantity η (p. 82), from which I have determined the position of the mean in the bay range. It is much easier to calculate, but of course not so exact, as we take no account of possible errors in the bay range itself or their correlation with errors in the median. I have accordingly tabulated its values in the last double column as a rough guide to the errors made in the numbers upon which the statements in the previous section depend. I shall return to the consideration of the probable errors below. Turning to columns 3 and 4 of our Table II., we can draw the following conclusions as to the variability of sex and class :—

(*a*.) *The Younger Generation is more Variable than the Old.*—Thus, foals are more variable than their sires, and, looking at the expressions in Table III. for the bay range, sires than grandsires. This is a rule I have now found true in a very great number of cases of inheritance. Parents are a fairly closely selected body of the general population, and so less variable than that population at large. This might appear pretty obvious in the case of thoroughbred horses when we are dealing with sires and grandsires. I have already pointed out that it was impossible to take 1000 to 1300 colts or fillies with as many independent sires, the fashion in sires is too marked; and of course the number of independent grandsires was still fewer.* But even in the case of dams, where we have taken as many independent dams as fillies, we see this reduction in variability in the older generation. As it also occurs with stature, &c., in man as well as with coat-colour in horses—in which latter case we expect artificial selection—it deserves special consideration. Without weighting with fertility, there exists a selection of the individuals destined to be parents in each generation. We have to ask whether the change in mean and variability from parent to offspring in each generation is secular or periodic, or to what extent it is partly one and partly the other. The importance of settling this point is very great; it concerns the stability of races. So far as my fairly numerous series of measurements yet go, I cannot say that a "stable population" has definitely shown itself; the characters of each race when measured for two generations seem to vary both in mean and standard deviation. Palæontologists tell us of species that have remained stable for thousands of years, but this is a judgment hitherto based on a *qualitative* appreciation. A quantitative comparison of the means, variabilities, and correlations of some living species in its present and its fossil representatives would be of the greatest interest and value. For myself, I must confess that my numerical investigations so far tend to impress me with the unstable character of most populations.

(*b.*) *There is fairly good evidence that the horse is more variable than the mare in coat-colour.* It would be idle to argue from the first four results of Table III. that the mare is more variable than the horse, in that these results show the dam to be more variable than the sire. For, as we have shown, the process of breeding and our method of extracting the data tend to produce a much more intense selection of sires than of dams. But if we compare the mean bay range in terms of the standard deviation of colts for our seven series of colts with that for the seven series of fillies in Table III., we find for the first 1·27458 σ_c and for the second 1·33854 σ_f. Hence we are justified in concluding that σ_c is greater than σ_f. In fact in only *one* case out of the seven does the series of fillies give a less variability than the corresponding series of colts, *i.e.*, colts corresponding to dams are somewhat less variable than fillies corresponding to dams. It must, however, be remembered that this conclusion is based upon the coat-colour of the animals recorded as yearling foals.† Thus, the coat-

---

* For some account of the extent of in and in breeding in the thoroughbred horse, see my memoir on "Reproductive Selection," 'Phil. Trans.,' A, vol. 192, p. 257 *et seq.*

† The reader must always bear in mind that when we speak of the variability of colour in sire or dam, &c., it means the variability of this class when they were yearlings.

colour may change both in intensity and variability with age, much as variability in stature changes with children from birth to adult life.

(*c.*) As a more or less natural result of (*b*) it follows *that any group, male or female, having male relatives is more variable than the same group with female relatives.* Thus sires of colts are more variable than sires of fillies; fillies half-sisters to colts are more variable than fillies half-sisters to fillies, &c. But out of the nine cases provided by our data there are three exceptions to the rule, and perhaps not much stress can be laid on it, at any rate in the above form. It would appear that males, relatives of males, are sensibly more variable than males relatives of females. The bay ranges are 1·3926 σ' and 1·4447 σ respectively, which indicates that the average σ' is larger than σ. But if we treat the groups of females alone, we find for females with male relatives the bay range = 1·3694 σ, and for females with female relatives 1·3433 σ', which indicates that the latter are more variable. The difference is, however, not very sensible. Possibly the rule is simply that extremes tend to produce their own sex, but our data are not sufficient for really definite conclusions on the point.

In order that we may have a fair appreciation of the probable errors of the quantities involved and the weight that is to be laid upon their differences, I place here a table* of the probable errors of η, of $\zeta = \sigma_x/\sigma_y$ and of r_{xy} for typical cases.

IV.—Table of Probable Errors.

Relations.	η_x	η_y	ζ	u	u'	r_{xy}
Sire and Filly . .	·0143	·0170	·0243	·0363	·0330	·0288
Grandsire and Colt	·0143	·0199	·0237	·0385	·0319	·0333
Colt and Colt . . (Whole siblings)	·0186	·0186	—	·0328	·0328	·0259
Filly and Colt . . (Half siblings)	·0179	·0185	·0315	·0335	·0328	·0363

It will be seen from this table that the probable error in η is about 3 per cent., in ζ about 2 to 4 per cent., in u about 2 to 2·5 per cent., and the values of r about ·03, growing somewhat larger as r grows smaller. The probable errors are thus somewhat larger than those which we obtain by the old processes when the characters are capable of quantitative measurement, but they are not so large as to seriously affect the use of the new processes in biological investigations. As we have already indicated, the probable errors of the η's may be roughly judged by Mr. SHEPPARD's formula for the median (p. 95).

It will be seen that the differences in the η's and ζ's of Table II., or the u's of

---

* I have to thank Mr. W. R. MACDONELL for friendly aid in the somewhat laborious arithmetic involved in calculating these probable errors.

Table III., are as a rule larger than the probable errors of the differences, sometimes several times larger. Yet in some cases they are not such large multiples of the probable errors of the differences that we can afford to lay great stress on the divergence of η or ζ or u in a pair of special cases. We must lay weight rather on the general tendency of the tables when all the series are taken together. Thus, while we may have small doubt about the correctness of (i.) of § 7 or (*b*) of § 8, we should look upon (iv.) of § 7 as an important suggestion which deserves serious consideration rather than a demonstrated law. The same again holds good for (*c*) of § 8. It is because of their suggestiveness that they are here included. That a differential fertility or an individualisation in the sex of offspring should be correlated with colour, would, if proved, be a fact of very considerable interest. It would again emphasise the important part which genetic selection plays in the modification of characters.* *À priori* it is not more unreasonable to expect coat-colour in horses than to suppose hair-colour in men to be correlated with fertility. But the fertility of man does seem to vary from the light to the dark races. The special feature of interest here, however, is that a different colour in the two sexes appears to influence the preponderance of one or other sex in the offspring. It would be an interesting inquiry to determine whether the sex-ratio in the offspring of "mixed marriages" varies when the races of the two parents are interchanged.

(9.) *On the Inheritance of Coat-colour in Thoroughbred Horses.*—(*a.*) *Direct Line. First Degree.*—Having regard to the probable errors—about ·03—in the values of the correlation coefficient r_{xy}, it seems quite reasonable to suppose that the mean parental correlation, actually ·5216, is practically ·5. It is quite impossible to imagine it the ·3 of Mr. GALTON'S view of the Law of Ancestral Heredity. If we adopt the view of that law given in my paper on the Law of Ancestral Heredity,† and take the coefficient γ to be different from unity, then it is shown in my paper on the Law of Reversion‡ that we cannot on the theory of blended inheritance get parental correlation as high as ·5 without values of the fraternal correlation which are much higher than those hitherto observed, certainly much higher than, as we shall see later, we find in the case of coat-colour in horses. Coat-colour in horses does not thus appear to be at all in accord with Mr. GALTON'S view of ancestral inheritance, or even with my generalised form of his theory. It does accord very well with what we might expect on the theory of exclusive inheritance as developed above, p. 91, on the assumption that there is no reversion.

Looking at the matter from the relative standpoint, we see that not much stress can be laid on the respective influences of the sire and dam on the colt, or of the sire and dam on the filly; but, on the other hand, the filly does appear to inherit more from

---

* See the concluding remarks in the memoir on "Genetic (Reproductive) Selection," 'Phil. Trans.,' A, vol. 192, pp. 257—330.

† 'Roy. Soc. Proc.,' vol. 62, p. 386 *et seq.*

‡ 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

both parents than the colt does. There is certainly (judged from coat-colour) no preponderance of the sire's influence over the dam's such as breeders appear occasionally to imagine. The average influence of the dam on the offspring indeed appears to be slightly greater than that of the sire, but the difference is of the order of the probable error, and not of the overwhelming character exhibited in the case of Basset Hounds. There is indeed in the case of thoroughbred horses not the same chance of carelessness produced by a misalliance afterwards screened by the defaulter. There exists, however, a far greater premium—considering the great value of yearlings from fashionable sires—set upon dishonesty. Again it is possible that when stallions receive too many public or private mares, or are still used in their old age, that they may, without losing the power of fertilising, lose some of the power of transmitting their characters. The divergences, so far as the probable errors are concerned, are not such that we are forced out of our way to explain them. With the single exception of sire and colt we see that our table shows the universal prevalence of the rule that:

Relatives of the same sex are more closely correlated than relatives of the same grades of the opposite sex. Thus:—

A colt is more like his sire than his dam.
A filly is more like her dam than her sire.
A dam is more like her filly than her colt.
A grandsire is more like his grand-colt than his grand-filly.
A colt is more like his brother colt than his sister filly.
A filly is more like her sister filly than her brother colt.

the latter two cases being true for both whole and half siblings.

The solitary exception is that a sire is more like his filly than his colt.

If we were to assume it a rule that a filly in the matter of coat-colour has stronger inheritance all round than a colt, we should find it agree with our results for parental inheritance, and receive considerable support for the much stronger correlation of fillies than of colts, when either whole or half siblings. But it would not be in accordance with our results for grandparents, for which, however, we have only details for two out of the eight possible cases. On the whole, I think we must content ourselves with the statements that parental correlation is certainly about ·5, and that with high probability each sex is more closely correlated with its own sex of the same grade of relationship.

(*b*.) *Direct Line, Second Degree.*—My data here are unfortunately only for two cases out of the possible eight. I hope some day to finish the series, but the labour of ascertaining from the studbooks the coat-colour of 700 or 800 separate sires is very great. Indeed it is not easy to follow up the pedigree through the male line when the sire is not one of the famous few. On the other hand, it is much easier through the female line. For this reason the *maternal* grandsire was taken. Even in this case we had to seek back for each sire—the year of whose birth was unknown—until we found the record of his coat-colour given under the heading of his dam in the year of his birth.

The average of our two cases gives a coefficient of correlation = ·3353, the colt having a greater degree of resemblance to the grandsire than the filly. This value is substantially greater than the ·25 we might expect for exclusive inheritance, and more than double the value ·15, to be expected for the grandparental correlation with Mr. GALTON's unmodified law for blended inheritance. Of course the ·25 is to be expected as the mean of the *eight* grandparental series, and, as we shall see for eye-colour in man, these may vary very much in magnitude. But allowing for this, it seems quite impossible that the average value could be reduced to ·15. I take it therefore that the grandparental, like the parental, data point to a law of inheritance other than that which has been described in my paper on the Law of Ancestral Heredity. This peculiar strengthening of the grandparental heritage has already been noted by me in my paper on the Law of Reversion,* and the difficulties of dealing with it on the principle of reversion therein discussed. There may be some opinion among breeders as to the desirability of emphasising the dam's strain in the choice of a sire which leads to this result, but if so it is unknown to me, nor do I see how it would work without also emphasising the correlation of the dam and foal. The mean value of the correlation for the maternal grandfather and grandchildren for eye-colour in man is ·3343—a result in capital agreement with that for coat-colour in horses. In that case the average of the eight series, as we shall see later, is considerably above ·25, and we must, I think, suspend our judgment as to whether this could possibly in the case of horses be the true mean value. As to the value ·15 it seems quite out of the question.

As already remarked, the influence of the maternal grandsire (unlike that of the sire) is substantially greater on the colt than on the filly.

(*c.*) *Collateral Heredity, First Degree.*—Here we have more ample data to go upon, namely, a complete set of six tables of both whole and half siblings of both sexes.

We notice one or two remarkable features straight off. In the first place, in the case of both fillies and colts, the whole siblings of the *same* sex have not a correlation the double of that of the half siblings, but have a correlation very considerably less than this. *À priori* we might very reasonably expect the one to be the double of the other. This is what would happen in the case of blended inheritance on the hypothesis of equipotency of the parents. As the half siblings are on the dam's side, we might assert a considerable prepotency of the dam over the sire. This cannot indeed be the explanation of the divergence in the case of Basset Hounds, where the half siblings have a correlation considerably *less* than half that of whole siblings,†

---

* 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

† 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

and yet the prepotency of the dam in coat-colour is very marked. But in the present case there is on the average only a slight, if indeed it be a real, prepotency of the dam. Further, if we turn to the correlation, no longer of siblings of the same sex, but of opposite sexes, we find the correlation of the whole siblings is approximately double that of the half siblings, as we should *à priori* have expected.

Taking averages on the assumption that the correlation for whole siblings should be double that for half siblings, we have the following results :—

Correlation between colts based on results for whole and half siblings .	·6667
Correlation between fillies based on results for whole and half siblings .	·7729
Correlation between filly and colt based on results for whole and half siblings	·5747
Mean correlation of siblings based upon all results for whole siblings .	·6329
Mean correlation of siblings based upon all results for half siblings . .	·7100
Mean correlation of siblings based upon results for both whole and half siblings	·6714

We can draw the following conclusions :—

(i.) In whatever manner we deduce the fraternal correlation it is very much larger than the ·4 for whole brethren, or the ·2 for half brethren, required by the unmodified Galtonian law. Such values, as we see above, could be deduced from the modified Galtonian law by taking γ greater than unity,* but this would involve values for the parental correlation sensibly less than those given by theory. We are again compelled to assert that the modified as well as the unmodified theory of blended inheritance, based on the Galtonian law, does not fit the facts. The above values, however, are quite compatible with the theory of exclusive inheritance on the assumption that there is an individual (not a sexual) prepotency from one pairing to another.

(ii.) In whatever way we consider it, it would appear that the average value of the fraternal correlation, as deduced from siblings with the same dam only, is greater than that deduced from siblings with both the same dam and the same sire.

I am not able to explain this in any way, for I cannot assert a very substantial prepotency of the dam. All I can say from the data at present available is that for horses and dogs there appears to be no simple numerical relation between the correlation of whole and half brethren.

(iii.) Offspring of the same sex are more alike than offspring of opposite sexes.

This appears to be generally true, so far as our data at present extend, and will be fairly manifest from the table below.

---

* 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

TABLE V.—Collateral Heredity.

Pair.	Man.			Dog.	Horse.	
					Coat-colour.	
	Stature.*	Cephalic Index.†	Eye-colour.‡	Coat-colour.§	Whole Siblings.	Half Siblings.
Brother-Brother	·3913	·3790	·5169	·5257	·6232	·3551
Sister-Sister	·4436	·4890	·4463		·6928	·4265
Brother-Sister	·3754	·3400	·4615		·5827	·2834

It will be noted that, with the single exception of eye-colour in man, sister and sister are more alike than brother and brother.

The mean value of the fraternal correlation for stature is ·4034, and for cephalic index ·4027. These results are in excellent accordance with the ·4 required by the Galtonian theory of blended inheritance. The mean values for eye-colour in man, coat-colour in dogs, and coat-colour in horses are: ·4749, ·5257, and ·6329. These are quite incompatible with that theory. I venture accordingly to suggest that we have here cases of an inheritance which does not blend, and that it is an inheritance which is far more closely described by the numbers we have obtained on the theory before developed of exclusive inheritance than by the law of ancestral heredity.

Taking in conjunction with these results for collateral heredity, those for parental and grandparental inheritance, we see that coat-colour in horses diverges widely from the laws which have been found sufficient in the cases of stature and cephalic index in man. The latter characters are really based on a complex system of parts, while the determination of coat-colour may depend on a simple or even single factor in the plasmic mechanism. Here Mr. GALTON'S suggestion of an exclusive inheritance of separate parts ('Natural Inheritance,' p. 139) may enable us to understand why stature and cephalic index differ so widely in their laws of inheritance from coat- and eye-colours.

PART III.—ON THE INHERITANCE OF EYE-COLOUR IN MAN.

(10.) *On the Extraction and Reduction of the Data.*—The eye-colour data used in this memoir were most generously placed at my disposal by Mr. FRANCIS GALTON. They are contained in a manuscript wherein, by a simple notation, we can see at a

---

* PEARSON, 'Phil. Trans.,' A, vol. 187, p. 253 *et seq.* See Note I. at the end of this paper.

† FAWCETT and PEARSON, 'Roy. Soc. Proc.,' vol. 62, p. 413 *et seq.*

‡ Present memoir, p. 113 *et seq.*

§ PEARSON, 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

glance the distribution in eye-colour of a whole family in its numerous male and female lines. Such complete details of the various direct and collateral relationships I have not hitherto come across, and from them I was able to form, in the course of some months of work, the twenty-four tables of correlation which are given in Appendix II. These tables, for the first time, give the whole eight series of grandparental and the whole eight series of avuncular relationships, besides such as we have deduced for other characters previously, *i.e.*, the four parental, the three fraternal relationships, and the table for assortative mating. The very great importance of this material will at once be obvious, and I cannot sufficiently express my gratitude to Mr. GALTON for allowing me to make free use of his valuable data.

At the same time we must pay due regard to the limitations of this material, which it is needful to enumerate, so that too great stress may not be laid on the irregularities and divergences which arise when we attempt to reduce the results to laws. These limitations are as follows :—

(*a.*) While the data of about 780 marriages are given in the record, they belong to less than 150 separate families. All our relationships, therefore, contain pairs weighted with the fertility of the individual families. Thus it was necessary to enter every child of a mother, every nephew of an uncle, and so forth. In the horse data we could take 1000 distinct mares and give to each one foal only. That is not possible in the present case.

(*b.*) The colour of eyes alters considerably with age. It is not clear that some of the eye-colours are not given for infants under twelve months, and certainly the eye-colours in the case of grandparents and others must have been taken in old, perhaps extreme old, age. In a large number of other cases of great grandfather, great great-grandfather, &c., great uncles, and so forth, the eye-colours must have been given from memory or taken from portraits—in neither alternative very trustworthy sources. Thus while the horse colour is always given for the yearling foal by the breeder, the eye-colour is given at very different ages, and comes through a variety of channels.

(*c.*) The personal equation in the statement of eye-colour, when the scale contains only a list of tint-names is, I think, very considerable. The issue for the collection of data of a plate of eye-colours like that of BERTRAND would be helpful, but we can hardly hope for a collection of family eye-colours so comprehensive as Mr. GALTON'S to be again made for a long time to come.

These causes seem to me to account for a good deal of the irregularity which appears in the numerical reduction of the results, but they are not, I hold, sufficient to largely impair the very great value of Mr. GALTON'S material.

In tabulating the data, I have followed the scale of tints adopted by Mr. GALTON, and I have used the entire material available in the cases of the grandparental, avuncular, and marital relations. I nearly exhausted the data for the parental relationships, but in these tables, which were first prepared, I stopped short at 1000 for the sake of whole numbers. I found, however, that it did not make the arithmetic sensibly shorter, and I afterwards dropped this limitation. In the case of brethren I took 1500 of each case—I daresay I could have got 2000 out of the records. As the light-eyed brethren are entered *first* in Mr. GALTON's MS., the First Brother in my unsymmetrical tables is always lighter-eyed than the Second Brother, hence the tables had to be rendered symmetrical by interchanging and adding rows and columns before we could reduce them. Thus the symmetrical tables have an apparent entry of 3000 pairs. Of course 1500 is the number used in finding the probable error of the correlation coefficient. The like difficulty does not occur in the brother-sister table, where indeed the difference of mean eye-colour for the two sexes would not allow of our making the table symmetrical. A comparison of the symmetrical with unsymmetrical tables for colts-colts and fillies-fillies, will show how little need there is for rendering the tables symmetrical when pairs are taken out of any similar class and tabulated without regard to the relative magnitude of the character in the two individuals of the pair, *i.e.*, WEATHERBY's record places the individuals simply in order of birth and not of darkness or lightness of coat-colour.

Table VII. gives the value of the chief numerical constants deduced from the twenty-four eye-colour tables in Appendix II.*

(11.) *On the Mean Eye-colour having regard to Sex and Generation.*—In order to test the degree of weight to be given to our conclusions, I have drawn up a table of probable errors for four typical cases—cases by no means selected to give the lowest possible values. Further, in Table VIII. I have given the probable error in the position of the median as determined in terms of the grey, blue-green range by the modification of Mr. SHEPPARD's formula (see p. 95). The grey, blue-green range of eye-colour is about one-fifth of the total observed range, so that the probable error in the position of the median varies from about ·4 to 1 per cent. of that range. This is not a large error, but, relative to the small variations of value with generation and sex, it is sensible, and we must not draw too fine conclusions on the basis of single inequalities.

TABLE VI.—Table of Probable Errors in Eye-colour Data.

Relations.	η_x	η_y	ζ	u	u'	r_{xy}
Mother and Son . .	·0253	·0188	·0431	·0267	·0256	·0283
Maternal Grandmother and Granddaughter .	·0348	·0350	·0767	·0276	·0314	·0361
Sister and Sister . .	·0244	·0244	—	·0216	·0216	·0234
Maternal Aunt and Nephew	·0230	·0186	·0414	·0255	·0250	·0302

---

* The theoretical formulæ by aid of which these constants were determined, have been indicated in the earlier part of this memoir, and in Part VII. of the present series on Evolution. The actual work of reduction has been most laborious, but I trust that our results are free from serious error.

If we examine this table we see that the error in η amounts to from ·02 to ·025 when we have upwards of 1000 tabulated cases, but can amount to ·035 when we have as few as 700 to 750 tabulated cases. An examination of the values of η in Table VII. shows us that most of our differences with probable errors taken on this scale are very sensible. A comparison with Table VIII. shows us that the probable error of the median is always greater than the probable error of η, and accordingly the former, being much easier of calculation, may be taken as a maximum limit. The probable errors of ζ, *i.e.*, the ratio of σ_x to σ_y, are more considerable, amounting to about ·04 for our longer series, and even to ·077 in the case of the short series of grandmother and granddaughter, but in this case ζ actually takes its maximum value of 1·291, so that the error is under 6 per cent.; in the longer series it is under 5 per cent. Again, we see that in most cases our differences in the ratio of variabilities are quite sensible. It must be admitted, however, that the ratio of variabilities as based on the grey blue-green range of eye-colour is not as satisfactory as that based on the bay range of coat-colour in horses. In the latter case, one-half of the horses fall into the bay range, but only about a quarter of mankind fall into the grey blue-green range of eye-colour, and, further, the appreciation of eye-colour seems to me by no means so satisfactory as that of coat-colour in horses.

I have tried a further series of values for the ratio of the variabilities by measuring the ranges occupied not only by the tints grey blue-green, but by the whole range of tints 3, 4, 5, and 6 of Mr. GALTON's classification (see p. 87). Lastly, I have taken a third method of appreciating the relative variabilities, namely, by using the method of column and row excesses, E_1 and E_2, discussed in Part VII. of this series. While this method has the advantage of using all and not part of the observations to determine the ratio of σ_x to σ_y, and so naturally agrees better with the results based on the four than the one tint ranges, it suffers from the evil that these excesses can only be found by interpolation methods, which are not very satisfactory when our classes are, as in this case, so few and so disproportionate. On the whole, this investigation of relative variability is the least satisfactory part of our eye-colour inquiry, and I attribute this to two sources:—

(i.) The vagueness in appreciation of eye-colour when no colour scale accompanies the directions for observation (*cf.* p. 103, (*c*)).

(ii.) A possible deviation from true normality in the factor upon which eye-colour really depends (*cf.* p. 80, (ii) 80).

Lastly, we may note that the probable error in the correlation amounts in most cases to less than ·03, rising only somewhat above this value for grandparental inheritance, where our series are somewhat short—650 to 750 instead of 1000. Here again most of the divergences are quite sensible.

Allowing accordingly for the comparative largeness of our probable errors, we shall do best to base conclusions on the general average of series; to insist on general inequalities rather than on exact quantitative differences, and to emphasise the

TABLE VII.—Eye-colour Inheritance in Man.

Pair of relatives.		Division of grey blue-green range by mean.		Ratio of variabilities.		Coefficient of correlation.	Coefficients of regression.		Number of cases.
x.	y.	η_x.	η_y.	σ_x/σ_y.	σ_y/σ_x.	r_{xy}.	R_{xy}.	R_{yx}.	N.
Father	Son	·5418	·5922	1·0667	·9375	·5503	·5870	·5159	1000
Father	Daughter . . .	·5064	·7322	1·1256	·8885	·4370	·4919	·3883	1000
Mother	Son	·8085	·5937	·9363	1·0680	·4817	·4510	·5145	1000
Mother	Daughter . . .	·8495	·7727	1·0188	·9815	·5096	·5192	·5002	1000
Brother	Brother	·6378	·6378	1	1	·5169	·5169	·5169	1500
Sister	Sister	·8827	·8827	1	1	·4463	·4463	·4463	1500
Brother	Sister	·6643	·8051	·9130	1·0953	·4615	·4213	·5055	1500
Husband	Wife	·4346	·7632	·9209	1·0859	·1002	·9227	1·0881	774
Paternal Grandfather .	Grandson . . .	·4665	·7135	1·0098	·9903	·4213	·4254	·4172	765
Paternal Grandfather .	Granddaughter .	·4698	·8134	1·0384	·9629	·3802	·3948	·3661	681
Maternal Grandfather .	Grandson . . .	·2154	·7129	·9122	1·0963	·3717	·3391	·4075	771
Maternal Grandfather .	Granddaughter .	·3115	·8652	·9675	1·0336	·2969	·2872	·3069	687
Paternal Grandmother .	Grandson . . .	·8491	·6733	·8659	1·1549	·2722	·2357	·3144	741
Paternal Grandmother .	Granddaughter .	·9493	·8156	·9259	1·0800	·2205	·2042	·2381	717
Maternal Grandmother .	Grandson . . .	·9371	·7159	1·1887	·8412	·2523	·2999	·2122	756
Maternal Grandmother .	Granddaughter .	·7673	·9090	1·2909	·7746	·3180	·4105	·2463	739
Paternal Uncle . . .	Nephew	·7387	·6402	·8815	1·1345	·3204	·2824	·3635	1290
Paternal Uncle . . .	Niece	·8087	·9063	·9874	1·0128	·2844	·2808	·2880	1128
Maternal Uncle . . .	Nephew	·4850	·7728	1·0192	·9812	·3706	·3777	·3636	1242
Maternal Uncle . . .	Niece	·4556	·8816	1·0520	·9506	·1938	·2039	·1842	1134
Paternal Aunt . . .	Nephew	·6982	·6563	·9012	1·1096	·2837	·2557	·3148	1186
Paternal Aunt . . .	Niece	·7988	·7539	1·1078	·9027	·1992	·2207	·1798	1149
Maternal Aunt . . .	Nephew	·8179	·6839	·9812	1·0192	·2576	·2528	·2625	1145
Maternal Aunt . . .	Niece	·7210	·7982	·9117	1·0968	·2101	·1915	·2304	1058

TABLE VIII.—On the relative Variability in Eye-colour.

Pair of relatives.		Ratio of variabilities from "excess."		Range of tint 3 in terms of σ. Range $= u\sigma$.		Range of tints 3, 4, 5, 6 in terms of σ. Range $= v\sigma$.		Probable error of median.	
x.	y.	σ_x/σ_y	σ_y/σ_x	u_x.	u_y.	v_x.	v_y.	x.	y.
Father	Son	·9981	1·0019	·6746	·7196	1·4950	1·5110	·0396	·0371
Father	Daughter	1·0532	·9495	·6189	·6966	1·3413	1·6178	·0432	·0384
Mother	Son	·9959	1·0041	·7617	·7132	1·6653	1·4904	·0351	·0375
Mother	Daughter	1·0424	·9593	·7178	·7313	1·5961	1·6500	·0372	·0366
Brother	Brother	1	1	·7759	·7759	1·5634	1·5634	·0199	·0199
Sister	Sister	1	1	·7347	·7347	1·6107	1·6107	·0210	·0210
Brother	Sister	·9917	1·0084	·8010	·7313	1·6492	1·5916	·0273	·0298
Husband	Wife	·9383	1·0657	·8061	·7423	1·7113	1·6203	·0377	·0409
Paternal Grandfather	Grandson	·9536	1·0487	·7939	·8017	1·3992	1·6008	·0385	·0381
Paternal Grandfather	Granddaughter	·9923	1·0077	·7144	·7418	1·3730	1·6793	·0453	·0437
Maternal Grandfather	Grandson	·9667	1·0344	·8120	·7407	1·6221	1·5528	·0366	·0411
Maternal Grandfather	Granddaughter	1·0775	·9281	·7990	·7730	1·4199	1·7836	·0404	·0417
Paternal Grandmother	Grandson	1·0242	·9764	·8882	·7691	1·6016	1·5846	·0350	·0404
Paternal Grandmother	Granddaughter	1·1019	·9075	·7925	·7338	1·5615	1·7600	·0398	·0430
Maternal Grandmother	Grandson	1·0197	·9807	·6332	·7527	1·6379	1·5891	·0486	·0408
Maternal Grandmother	Granddaughter	1·1519	·8681	·5922	·7645	1·4447	1·7965	·0525	·0407
Paternal Uncle	Nephew	1·0179	·9825	·8242	·7265	1·4636	1·5268	·0286	·0324
Paternal Uncle	Niece	1·1728	·8527	·7695	·7598	1·4253	1·8304	·0327	·0331
Maternal Uncle	Nephew	·9984	1·0016	·7977	·8130	1·5620	1·5763	·0301	·0295
Maternal Uncle	Niece	1·0154	·9849	·7468	·7856	1·4396	1·8208	·0336	·0320
Paternal Aunt	Nephew	·9964	1·0036	·8208	·7397	1·6311	1·5929	·0299	·0332
Paternal Aunt	Niece	1·1804	·8472	·7126	·7894	1·4974	1·8097	·0350	·0316
Maternal Aunt	Nephew	·9332	1·0716	·8022	·7871	1·7337	1·5371	·0311	·0317
Maternal Aunt	Niece	1·0730	·9320	·8925	·8137	1·7202	1·7873	·0291	·0319

general tendency of a series rather than pick out single differences for special consideration. If we do this we shall still find that remarkable results flow from our Tables VII. and VIII., most of which seem hitherto to have escaped attention.

I return now to the special topic of the present section, the mean eye-colour, after this lengthy—if needful—digression on the probable error of the data given in our tables.

We may, I think, safely draw the following conclusions :—

(*a.*) *Man has a mean eye-colour very substantially lighter than that of woman.*

If we compare the mean eye-colour of father with mother, of son with daughter, of brother with sister, of grandfather with mother, of uncle with aunt, of grandson with granddaughter, of nephew with niece, we have the same result—man is distinctly lighter eyed than woman.

(*b.*) *There appears to be a secular change taking place in eye-colour, but this is more marked and definite in the man than in the woman.*

Thus we have the following mean values for η in classes, which must roughly represent successive generations :—

Grandfather	·3658	·4449	Grandmother	·8757	·8523
Father	·5241		Mother	·8290	
Son	·5929	·6484	Daughter	·7524	·8016
Grandson	·7039		Granddaughter	·8508	

Another comparison may be made by noting that grandsons are darker than grandfathers, sons than fathers, nephews than uncles. Similarly, granddaughters are lighter than grandmothers, daughters than mothers, but nieces are not lighter than aunts, as we might have expected. Thus, while the records show a definite darkening of the eyes of men, there appears to be a certain but less sensible lightening of the eyes of women. Again, the younger generations are much closer in eye-colour than the older generations. The difference in eye-colour between grandsons and granddaughters, sons and daughters, nephews and nieces is only about 15 per cent. of the grey blue-green range, but for fathers and mothers it is 30 per cent., and for grandfathers and grandmothers 50 per cent.

When we realise that difference in eye-colour appears to be a sexual character, the true explanation of this secular change in eye-colour becomes still more obscure.

If the lighter eye-colour of the older generation be due to an effect of old age, why is it conspicuous only in the male and not in the female? Why is the mother sensibly darker than the daughter, but the father sensibly lighter than the son?

Further, supposing light eyes much commoner among our grandfathers than among their grandsons, and dark eyes among our grandmothers than among their granddaughters, we cannot attribute the great approach in eye-colour to a blending of the parental characters, for, as we shall see later, eye-colour does not seem to blend, it is rather an exclusive character. We should, therefore, be thrown back on prepotency of the mother—a conclusion possibly warranted by our results in the case of daughters, but not in the case of sons. Again, why was there such a marked difference in eye-colour between the men and women of three or four generations back?* And if it was a sexual character, why is it disappearing? Was it not, perhaps, a racial difference? Light and dark eyes are not unusually associated with distinct races, and it is just possible that the change in eye-colour is a product of reproductive selection; the old blue-eyed element of the population may be dwindling owing to the greater fertility of the women of dark-eyed race, and thus without any obvious struggle for existence and survival of the fitter, the blue-eyed race may be disappearing from England, as the Langobard type has so largely gone from Italy and the Frank from France.† It will not do to be dogmatic about these matters, but the more one measures characters in different generations, the less stable do races appear to be. We speak of the national characters of the Englishman or the Frenchman based upon our experience of how these races have acted in past history, but although there has been no great racial invasion nor struggle, can we safely assert the physical characters of the Englishman to-day do not differ substantially from those of the Englishman of the Commonwealth? It seems to me that the possibly continuous change of characters in a race, not subjected to very apparent internal or external struggle, is a problem of the highest interest to the anthropologist and ultimately to the statesman.

Whatever be the explanation of this secular change in eye-colour, it appears to correspond singularly enough to the secular change we have noted in the coat-colour of thoroughbred horses—in the older generation the sexes differ more widely than in the younger.

(c.) *The maternal male relative (grandfather and uncle) is substantially lighter-eyed than the paternal male relative (grandfather and uncle).*—I see no explanation for this curious result, but it seems worth while to specially note it, for there are curious anomalies in the inheritance through the various male and female lines which may find their complete explanation some day when more and possibly more trustworthy characters have been investigated.

(12.) *On the Variability of Eye-colour with reference to Sex and Class.*—The determination of the relative variability of not exactly measurable characters is, as we have already seen (p. 105), a somewhat delicate problem. It is more so in the case of eye-colour in man than of coat-colour in horses, for there is greater difference in the means, and accordingly the ratio of σ_x/σ_y, as found from the ratio of the "excesses" (p. 105), will be even less reliable.‡ The class indices corresponding to the

---

* Mr. GALTON'S records went back to great-grandfathers, many of whom accordingly appear in our data for grandfathers.

† See Note II. at the end of this paper.

‡ The relative variability of all classes was worked out for thorough-bred horses by the "excess" method, and in only one case—that of dam and colt—did it differ from the bay range method in its determination of the class with the greater variability.

grey blue-green range are also not entirely satisfactory in their results, nor those taken for a still larger range covering tints 3, 4, 5, and 6, or blue-green, grey, hazel, light brown, and brown, which cover roughly about 1·5 to 1·6 times the standard deviation. We shall now consider the results of three methods of considering the relative variability, (α) from the excesses given in columns 1 and 2 of Table VIII.; (β) from the grey blue-green range given in columns 3 and 4 of Table VIII.; and (γ) from the range of tints 3 to 6 inclusive given in columns 5 and 6 of Table VIII. As we have already indicated, these methods are not likely to give the same relative magnitude numerically for the variabilities; we must content ourselves if they agree in making the ratio of σ_x to σ_y greater or less than unity. Now, in the twenty-two cases

α and β disagree in 10 cases.
β and γ disagree in 7 cases.
α and γ disagree in 5 cases.

Further, for the five cases in which α and γ disagree, those for father and son, paternal grandfather and grandson, maternal uncle and nephew, show so little difference of variability in the two sexes that both methods give sensibly the same results, *i.e.*, equality of variability. In the cases of the paternal grandfather and grandchildren, the two methods diverge rather markedly.

It will be of interest accordingly to work out the probable errors as given by the excess method for one, say the first of these cases. The theory is given in Part VII. of the present series. Here $E_1 = 275·165$, $E_2 = 309·013$, whence we find probable error of $E_1 = 17·273$, probable error of $E_2 = 16·925$, correlation between errors in E_1 and $E_2 = -·4424$, probable error in $\sigma_1/\sigma_2 = ·0394$.

Thus the probable error in the ratio of the variabilities is about 4 per cent., and of the order of the quantities by which we are distinguishing the relative size of σ_1 and σ_2.

Further, there is another source of error in evaluating E_1 and E_2 due to the method of interpolation used, and this would still further increase the probable error in σ_1/σ_2. We cannot therefore lay any very great stress on the manner in which the ratios of variabilities for the paternal grandfather and grandchildren have swung round from (α) to (γ).

A further examination shows us that in all five cases wherein γ differs from α it is in accord with β. I shall accordingly take γ as the standard criterion, but in those cases in which it has agreement with α, its conclusions must be given greater weight.

(*a*.) *On the Relative Variability of Sex in Eye-colour.*—The following male groups are more variable than the corresponding female groups:—

Sons of fathers than daughters of fathers.
Sons of mothers than daughters of mothers.
Brothers of brothers than sisters of sisters.

Grandsons (in four series) than granddaughters (in four same series).
Nephews (in four series) than nieces (in four same series).
Fathers (in two series) than mothers (in two series).
Grandfathers (in four series) than grandmothers (in four like series).
Uncles (in four series) than aunts (in four like series).

The following female groups are more variable than the corresponding male groups :—

Sisters of brothers than brothers of sisters.
Wives than husbands.

We have thus 21 series with male preponderance against only two with female preponderance of variability.

Again, the mean range of tints 3, 4, 5, 6 in 22 male series equals 1·5424 σ_x, and in 22 female series equals 1·6740 σ_y, or we have enough evidence to show that the ratio of male to female variability is about 1·08.*

This greater variability of the male in eye-colour is of considerable interest. It does not appear to be a result of sexual selection, for so far as our comparatively small series weighs, husbands are less variable than wives. That mothers are, however, less variable than fathers seems to indicate that dark-eyed women are more fertile† than light-eyed, for we must bear in mind that mothers have on the average a darker eye-colour than wives. We have thus again reached the same conclusion as before, namely, that a dark-eyed element in the population with a prepotent fertility is replacing the blue-eyed element.

The other female exception to the general rule of greater variability in the eye-colour of the male is that in mixed families the sisters appear to be more variable than their brothers, notwithstanding that brothers of brothers are more variable than sisters of sisters. In other words, so far as eye-colour is concerned an exceptional man is more likely to have brothers than sisters, but an exceptional woman also is more likely to have brothers than sisters. The inference is not very strong, as the excess method (α) makes brothers of sisters and sisters of brothers of sensibly equal variability; it rests therefore on (β) and (γ) only. Still it deserves fuller investigation.

(*b*.) Let A and B be two grades of relationship, of which A refers to the older generation, and A and B refer to either sex. Then the variability of all the A's

---

* It is worth noting that the ratio of male to female variability in the coat-colour of horses is 1·05 (see p. 96). In both cases the female is darker, *i.e.*, has less of "colour"; thus if we could take a coefficient of variation ratio instead of standard deviation ratio as the test, we should find the difference of variability less, possibly even zero.

† For if mothers are to be less variable than wives, their distribution must be more compressed round the mean than that of wives; this denotes that fertility is correlated with eye-colour, and the darker eye-colour goes with the greater fertility. [See Note II. at end of memoir, however.]

who have female B's is invariably greater than the variability of all the A's who have male B's.

The law appears to be universal, at least it is absolutely true for all the 10 cases to which we can apply it. Thus the father of sons is less variable than the father of daughters, the maternal grandmother of grandsons less variable than the maternal grandmother of granddaughters, or the paternal uncle of nephews less variable than the paternal uncle of nieces. In other words, although women appear, in eye-colour, to be less variable than men, they spring from more variable stocks.

This law is a remarkable one, but in face of the evidence for it, it seems difficult to doubt its validity. Should it be true for more characters in man than eye-colour,* the conclusions to be drawn from it will be somewhat far-reaching, however difficult it may be to interpret its physiological significance.

(*c.*) *On the Relative Variability of Different Generations.*—We have already had occasion to refer to the general rule that the older generation will be found less variable than the younger, for it is in itself a selection, namely, of those able to survive and reproduce themselves. But this rule is obscured in the present case by several extraneous factors, thus :—

(i.) The male is sensibly more variable than the female, consequently it is quite possible that an elder male generation should appear more variable than a younger female generation.

(ii.) There appears to be a secular change in eye-colour going on. Thus while the grandparental population is a selection from the general population, the general population, at a given time, is a selection from that of an earlier period.

Thus, taking means in the cases of the grandparental and avuncular relationships, we have from (γ) the following results :—

The father is more variable than son and than daughter.
The mother is less variable than son and more than daughter.
The grandfather is more variable than grandson and than granddaughter.
The grandmother is less variable than grandson and more than granddaughter.
The uncle is more variable than nephew and more than niece.
The aunt is less variable than nephew and more than niece.

In other words, the older generation is always more variable than the younger, except when rule (α), that the male is more variable than the female, comes in to overturn this law. If we confine ourselves to comparisons of the same sex the rule is seen to be universal.

We are thus forced again to ask for an explanation of the decreasing variability of eye-colour, and can only seek it in that secular change we have several times had

---

* Fathers of daughters are more variable in stature than fathers of sons ('Phil. Trans.,' A, vol. 187, p. 274). I propose to reinvestigate the question with regard to mothers from the material of my family measurement cards, which is far more extensive than the material I had at my disposal in 1895.

occasion to refer to. Mean and standard deviation of eye-colour appear to have changed sensibly during the few generations covered by Mr. GALTON'S eye data.

It is difficult to understand how any obscurity about the recording of eye-colours could lead to anything but chaos in the numerical results. It does not seem to me possible that such results as we have reached under (*a*), (*b*), and (*c*), namely, greater variability in the male, greater variability in the stock of the female, and secular change in variability, can be due to any process of recording. I am forced to the conclusion that they are peculiar to the character under investigation, and are not due to the manner of taking the record or of dealing with it arithmetically. I have purposely avoided drawing attention to small differences and forming any conclusions which did not depend on whole series of groups and substantial averages.

(13.) *On the Inheritance of Eye-colour.* (*a.*) *Assortative Mating.*—Before we enter on the problem of inheritance, it is as well to look at the substantial correlation obtained between the eye-colour in husband and wife. When in 1895 I reached the value ·0931 ± ·0473 for stature, I wrote, "we are justified in considering that there is a definite amount of assortative mating with regard to height going on in the middle classes."* Since then we have worked out the coefficients of correlation in stature, forearm, and span for 1000 husbands and wives (instead of 200) from my family data† cards. The results, which are very substantial, will be dealt with in another paper, and amply confirm my view that assortative mating is very real in the case of mankind. The value (·0931) cited above is in close agreement with the result now reached (·1002 ± ·0378) for eye-colour in the *same* material. The correlation between husband and wife for two very divergent characters is thus shown to be about ·1, or is 25 *per cent. greater than is required between first cousins*‡ *by the law of ancestral heredity.*

This remarkable degree of likeness between husband and wife—the scientific demonstration that like seeks like—cannot be overlooked. It shows that sexual selection, at least as far as assortative mating is concerned, is a real factor of evolution, and that we must follow DARWIN rather than WALLACE in this matter.§

(*b.*) *Collateral Heredity. First Degree.*—I deal first with this form of heredity, as it offers least points for discussion. The values of the correlation ·5169 for brothers, and ·4463 for sisters and sisters are considerably less than what we have found for coat-colour in horses, but, like the value ·4615 for brothers and sisters, are substantially greater than ·4 to be expected from the unmodified Galtonian law. They could be reached by making γ greater than unity in my statement of the law of ancestral heredity.|| They could also be given by the law of exclusive inheritance

---

* 'Phil. Trans.,' A, vol. 187, p. 273.

† See also 'Grammar of Science,' second edition, pp. 429–437.

‡ 'Roy. Soc. Proc.,' vol. 62, p. 410.

§ 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

|| I have considered possible explanations of this apparently large assortative mating (i.) in both stature

(see p. 90) with a certain degree of prepotency in the individual pairing. As we have already noted, collateral inheritance of the first degree alone considered will not enable us to discriminate between blended and exclusive inheritance.

We note that the male in collateral inheritance predominates over the female, brothers being more alike than sisters in eye-colour, and brother and sister more alike than sister and sister. The mean value for inheritance in the same sex is, however, greater than the value for inheritance between opposite sexes (*cf.* p. 102).

(*c.*) *Collateral Heredity. Second Degree.*—A very cursory inspection of the coefficients of correlation for the eight series of avuncular relationships shows us that it is quite impossible that the mean value should be ·15 as required by the Galtonian Law. The average value of the avuncular correlation is ·2650, and of the regression of nephew and niece on uncle or aunt is ·2733. The probable error of the former result will not be more than ·02, and of the latter something greater, as the ratio of the variabilities is open to larger error. This mean value is accordingly, within the limits of errors of investigation, identical with the ·25 to be expected on the theory of exclusive inheritance. It is a value which appears to be quite impossible on the theory of blended inheritance even with my generalised form of the ancestral law.

We may draw several other important conclusions from our table of avuncular correlations:—

(i.) Nephews are more closely related to both uncles and aunts than nieces are. This is true in each individual case, whether it be judged by correlation or regression. The mean correlations for uncles and for aunts are as ·3081 to ·2219 respectively.

(ii.) Uncles are more closely related to nephews and nieces than aunts are. This is true for three out of the four individual cases; in the fourth case the difference is of the order of the probable error of the difference. The mean correlations of nephews and nieces are as ·2923 and ·2377 respectively.

(iii.) Paternal uncles and aunts are more closely correlated with their nieces and nephews than maternal uncles and aunts. The mean values are as ·2719 to ·2580.

(iv.) Resemblance between individuals of the same sex is closer than between individuals of opposite sex. The mean values for the avuncular correlation in the same sex and in the opposite sex are respectively ·2751 and ·2549.

(v.) Uncles are more closely related to nephews than aunts to nieces (mean correlations as ·3455 to ·2046). In fact, generally, we see a very considerable preponderance of heredity in the male line so far as these avuncular relations for

---

and eye-colour, being characters of local races, or even families, and the husband seeking his wife in his own locality or kin; (ii.) in a possible correlation of homogamy and fertility. See 'Roy. Soc. Proc.,' vol. 66, p. 28. Neither seem very satisfactory. Consciously or unconsciously, man and woman appear to select their own type in eye-colour and stature, until they are apparently more alike than such close blood relations as first cousins! Until we know how far this correlation extends to other characters, it would, perhaps, be idle to draw conclusions as to its bearing on widely current views as to first cousin marriages.

eye-colour extend. It is noteworthy that while the two highest correlations are reached for nephew with paternal and with maternal uncles, nearly the two lowest are found for niece with paternal and with maternal aunts. Without laying special stress on each small difference, it must be admitted that the avuncular correlations vary in a remarkable manner with sex, and differ very widely from the practical equality of resemblance which we might *à priori* have expected to exist in this relationship.

(*d.*) *Direct Heredity. First Degree.*—Here we have a mean value of the paternal correlation = ·4947. This is in excellent agreement with the ·5 to be expected by our theory of exclusive inheritance; it is thus in practical agreement with the value of the parental correlation obtained for the inheritance of coat-colour in horses. It would not be inconsistent with a high value for γ in the theory of blended inheritance, but such a value of γ is rendered impossible by the values we have obtained for collateral heredity (see 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*).

We may draw the following special conclusions:—(i.) The son inherits more strongly from his parents than the daughter, the mean correlations are as ·5160 to ·4733; (ii.) The son inherits more strongly from his father than his mother, and the daughter more strongly from her mother than her father.

This is part of the general principle which we have seen to hold, namely: that change of sex weakens the intensity of heredity.

The correlation of father and daughter appears to be abnormally below the other three, but something of the same kind has been noted in certain stature data; as it is, the high correlation of father and son renders the mean paternal correlation with offspring (·4936) sensibly equal to the mean maternal correlation (·4956).

(*e.*) *Direct Heredity. Second Degree.*—If we take the mean value of the eight grandparental correlations, we find it equals ·3164, while the mean value of the regression of offspring on their grandparents is ·3136. These results are absolutely incompatible with the ·15 required by Mr. GALTON's unmodified theory, and they in fact put the theory of blended inheritance entirely out of court. At the same time, unlike the cases of parental, avuncular, and fraternal inheritance, they cannot be said to be in good agreement with the value ·25 required by the theory of exclusive inheritance. We have to admit that our grandparental data are shorter series than in the other cases, and that guesses as to grandparents' eye-colour, based on memory, miniatures, &c., were more likely to be made. Further, such guesses might easily be biased by a knowledge of the eye-colour of more recent members of the family. Still a reduction from ·32 to ·25 is a very large reduction, and we have to remember that for long series in the case of the thoroughbred horses, with no such guessing at colour as may occur with ancestors' eyes, we found ·3353 for the maternal grandsires, a result in excellent agreement with the ·3343 found for the maternal grandfathers in the present case. Thus while the theory of exclusive inheritance *without reversion* suffices to describe the quantitative values we have found for the parental, the avuncular and the fraternal correlation in the cases of both horse and man, it is yet in both these cases unsatisfactory so far as the grandparental inheritance is concerned. It may be imagined that if we allowed for reversion, we might emphasise the grandparental correlation beyond the value ·25 suggested by theory. But I have shown in my memoir on the "Law of Reversion," that with the parental correlation as high as ·5, we cannot hope to have the grandparental correlation even with reversion higher than ·25. (See 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*) Clearly the values obtained for grandparental correlation in this paper—the first I believe hitherto investigated—seem to present anomalies which our theory of blended inheritance totally fails to account for, and which may require some modification of our views on reversion before we can meet them on our theory of exclusive inheritance.

I note the following general results deduced from our values of the grandparental correlations :—

(i.) Grandsons are more closely correlated with both grandparents than granddaughters are. This is true for three out of the four cases; the exception, maternal grandmother, is covered by another rule (iv.). The mean correlation for grandparents and grandsons is ·3294, and for grandparents and granddaughters ·3039.

(ii.) Grandfathers are more closely correlated with grandchildren than grandmothers are. This is true in three out of the four cases, the fourth being again subject to rule (iv.). The mean correlations for grandfathers and grandmothers are ·3675 and ·2658 respectively.

(iii.) Paternal grandparents appear to be more closely correlated with their grandchildren than maternal grandparents, the average values of the two correlations being ·3236 and ·3097 respectively.

(iv.) Resemblance between individuals of the same sex is closer than between individuals of the opposite sex. The mean values for the grandparental and grandchild correlation in the same and the opposite sexes are ·3329 and ·3004 respectively.

(v.) Grandfathers are more closely related to grandsons than grandmothers to granddaughters, the mean correlations being as ·3965 and ·2693 respectively. It will be noted at once that these five rules are identical with those we have obtained for the avuncular correlations. So that there is small doubt that they are general rules relating to all grades of relationship for this character.

It seems to me probable that the correct form of (iii.) is : Paternal grandfathers are more highly correlated with grandchildren (·4006) than maternal grandfathers (·3343), and paternal grandmothers (·2468) less highly correlated than maternal grandmothers (·2851). I have not stated the rule in this form, because it is not confirmed by the corresponding results for uncles and aunts. Paternal uncles (·3024) are more closely correlated with nephews and nieces than maternal uncles (·2722), but paternal aunts (·2414) are slightly more instead of less correlated with nephews and nieces than maternal aunts (·2338). I consider, however, that the correlation of paternal aunt and nephew (·2837) in our series is abnormally high.

Now it will, I believe, be seen that the investigation of the eight avuncular and the eight grandparental relationships, here made for the first time,* enables us to draw far wider conclusions than when, as hitherto, only parental and fraternal correlations are dealt with. In making the subjoined general statements, however, I must emphasise the following limitations :—

(α.) The rules are deduced only from data for one character in one type of life.

(β.) This character appears to be undergoing a secular change, a change very possibly due to a correlation between eye-colour and fertility in woman. Thus such a change might not unlikely differentiate the male and female influences in heredity.

My conclusions, definitely true for eye-colour in man, and at the very least suggestive for investigations on other characters in other types of life, are :—

(i.) That the younger generation takes, as a whole, more after its male than its female ascendants and collaterals.

(ii.) That the younger generation is more highly correlated with an ascendant or collateral of the same than of the opposite sex.

(iii.) That the younger generation is more highly correlated with an ascendant or higher collateral reached by a line passing through one sex only than if the line changes sex.

Thus correlation is greater with a paternal uncle than with a maternal uncle, or with a maternal grandmother than a paternal grandmother.

(iv.) Males are more highly correlated with their ascendants and collaterals than females are.

The above rules apply to the *averages;* individual exceptions will be generally found to arise from a conflict of rules. Thus (ii.) and (iii.) may in special cases come into conflict with (i.). When we have more data for a greater variety of characters, we shall see better the relative weight of these rules in cases where they conflict.

(*f.*) *Exclusive Inheritance in Eye-Colour.*—A cursory examination of the eye-colour records shows at once how rare is a blend of the parental tints. Even when such is recorded, it is by no means clear that we have not to deal with a medium tint which is really a case of reversion to a medium tinted ancestor. The failure of eye-colour to blend is, I think, well illustrated by what Mr. GALTON has termed cases of "particulate" inheritance. In the thousands of eye-colours I have been through, I noticed some half-dozen cases only in which the two eyes of the same individual were of different tint, or the iris of one pupil had streaks of a second tint upon it.†

---

* I anticipate equally valuable results when characters are first correlated for the nine possible cousin series.

† In the same manner the occurrence of particulate inheritance in coat-colour in horses may be really an argument against the existence of blends. In the many volumes of the studbooks I have examined, the recorded instances of piebalds are vanishingly few in number.

If we allow that it is from the theory of exclusive inheritance that we must seek results in the present cases, we see that for parental, collateral, and avuncular relationships we get quite excellent results, but that the grandparental relationship is somewhat anomalous. *À priori* it might appear that reversion would aid us in increasing the correlation between offspring and remote ascendants. But, as I have shown elsewhere,* this superficial view of reversion forgets that the parents as well as the offspring revert, and if we increase the grandparental correlation above ·25, we at once reach difficulties in the values of the parental correlation, provided we adopt what appear to be reasonable assumptions as to reversion being a continuous and decreasing factor from stage to stage of ancestry. I am inclined accordingly to suspend judgment on the grandparental relationships, thinking that the smallness of the number of families dealt with in Mr. GALTON'S data (200) may have something to do with my peculiar results. Meanwhile I shall endeavour to get the remaining six grandparental tables for thoroughbred horses worked out, and see whether they confirm the high values already found for the two maternal grandsires and offspring, or give an average value much nearer ·25.

That the reader may see at a glance the general results hitherto obtained in this and other papers, I append the following table of inheritance:—

---

* See my paper on "The Law of Reversion," 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.* Also 'The Grammar of Science,' second edition, 1900, pp. 486–96, "On Exclusive Inheritance."

TABLE IX.—Theoretical and Actual Results for Inheritance.

Relationship.	Theory.		Man.			Horse.	Hound.	Daphnia.
	Blended inheritance.[1]	Exclusive inheritance.[2]	Stature[3].	Head index.[4]	Eye-colour.[5]	Coat-colour.[6]	Coat-colour.[7]	Spine.[8]
Parental	·3000	·5000	·3355	·3348	·4947	·5216	·3507	[·3295]
Mid-parental . . .	·4242	—	·4745	·4735	—	—	—	·4660
Grandparental . .	·1500	·2500	—	—	·3166	·3353	·1340	[·1360]
G. Grandparental .	·0750	·1250	—	—	—	—	·0404	—
Avuncular . . .	·1500	·2500	—	—	·2650	—	—	—
Whole sibling . .	·4000	·4 to 1·0	·4034	·4025	·4749	·6329	·5170	·6934
Half sibling . . .	·2000	·2 to ·5	—	—	—	·3550	·1646	—

[1] Mr. GALTON'S unmodified hypothesis. See "Law of Ancestral Heredity," 'Roy. Soc. Proc.,' vol. 62, p. 397.

[2] Without any reversion. See "Law of Reversion," 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.* The values for the fraternal correlation depend on the degree of prepotency of either parent within the union.

[3] See 'Phil. Trans.,' A, vol. 187, p. 270.

[4] See 'Roy. Soc. Proc.,' vol. 62, p. 413. The paternal correlations, for reasons stated in the paper, are excluded from the result.

[5] See p. 113 *et seq.* of the present memoir.

[6] See p. 98 *et seq.* of the present memoir. The grandparental correlation is based on two cases only.

[7] See 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

[8] See 'Roy. Soc. Proc.,' vol. 65, p. 154. I have deduced the value for parents and grandparents from Dr. WARREN'S results for midparent and midgrandparent. The value for whole siblings I obtained from Dr. WARREN'S measurements, which he with great kindness placed at my disposal.

(14.) *Conclusions.*—The course of this investigation has not been without difficulties, and I am fully prepared to admit that more obscurity and greater probable errors are likely to arise when we deal with the inheritance of a character not directly measurable, than when we take that of a character to which we can at once apply a quantitative scale. But I contend that many of the characters, the inheritance of which it is most important to investigate, do not at present, and perhaps never will, admit of a quantitative measurement. We can arrange in order, we can classify, we can say more or less intense, but we cannot read off value on a scale. It is just such characters also, which the not highly trained observer can most easily appreciate and record. Hence we have been compelled to devise some method of dealing with them, and the present paper illustrates how the method invented can be applied to reach results of considerable interest and of substantial validity.

In order to illustrate the method, I chose two characters, coat-colour in horses and eye-colour in man, which seemed sufficiently diverse both as to origin and species.* The new method enabled me to reach results for half-brethren, grandparents and uncles and aunts, which had not yet been independently considered. The conclusions arrived at for eye-colour in man at no point conflict with those for coat-colour in horses, and both in the main accord with the theory of exclusive inheritance without reversion herein developed. We find—

(i.) No approach to a single value for the coefficient of inheritance for each grade of relationship; it varies widely with the sex, and the line through which the relationship is traced.

(ii.) No approach in average values to those which would be indicated by Mr. GALTON'S Law.

Nor does the modification of Mr. GALTON'S Law, which I have termed the Law of Ancestral Heredity, give better results. For, if we cause it to give the parental values, it then renders results inconsistent with the fraternal values.

(iii.) There is agreement with the theory of exclusive inheritance without reversion for the parental, avuncular and fraternal series; but there is some anomaly in the case of grandparental inheritance. This requires further investigation, and possibly a modification of our views on the nature of reversion.

We want a list formed of characters in various types of life, which are supposed to be exclusively inherited, and then experiments ought to be made and statistics collected with regard to these characters. It is in this field of exclusive inheritance that we must look for real light on the problem of reversion.

If we consider the three known forms of inheritance, the blended, the exclusive, and the particulate (which may possibly be combined in one individual, if we deal with different organs); if we consider further that these forms may possibly have to be supplemented by others not yet recognised (*e.g.*, reversional theories depending, say, on heterogamous unions), then it would appear that the time is hardly ripe even for provisional *mechanical* theories of heredity. What we require to know first is, the class of organs and the types of life for which one or other form of inheritance predominates. As variation in no wise depends on the existence of *two* germ-plasms, so biparental heredity can by no means be treated as the result of their simple quantitative mixture; the component parts of these germ-plasms corresponding to special characters and organs, must be able to act upon each other in a variety of qualitatively different ways. To adopt for a moment the language of DARWIN'S theory of pangenesis, the multiplying gemmules from an organ in the father must (i.) cross with gemmules from that organ in the mother, and the hybrid gemmules give rise to blended inheritance, (ii.) must without crossing multiply alongside the gemmules of the mother, and give rise to particulate inheritance, (iii.) must alone survive, or alone

---

* Since supplemented by my investigations, based on Mr. GALTON'S data, for coat-colour in hounds, 'Roy. Soc. Proc.,' vol. 66, p. 140 *et seq.*

be destroyed in a struggle for existence with those of the mother, and give rise to exclusive inheritance. And all these three processes may be going on within the same germ-plasm mixture at the same time! Even without using the language of gemmules, processes analogous to the above must be supposed to take place. Thus a quantitative "mixture of germ-plasms" becomes a mere name, screening a whole range of mechanical processes; and very possibly a new one could be found for each new form of heredity as it occurs. Such processes like the old ones would still remain without demonstrable reality under the veil of "mixture of germ-plasms."

What I venture to think we require at present is not a hypothetical plasmic mechanics, but careful classifications of inheritance for the several grades of relationship, for a great variety of characters, and for many types of life. This will require not only the formation of records and extensive breeding experiments, but ultimately statistics and most laborious arithmetic. Till we know what class of characters blend, and what class of characters is mutually exclusive, we have not within our cognizance the veriest outlines of the phenomena which the inventors of plasmic mechanisms are in such haste to account for. Such inventors are like planetary theorists rushing to prescribe a law of attraction for planets, the very orbital forms of which they have not first ascertained and described. Without the observations of TYCHO BRAHÉ, followed by the arithmetic of KEPLER, no NEWTON had been possible. The numerical laws for the intensity of inheritance must first be discovered from wide observation before plasmic mechanics can be anything but the purest hypothetical speculation.

APPENDIX I.

Tables of Colour Inheritance in Thoroughbred Racehorses, extracted by Mr. LESLIE BRAMLEY-MOORE from WEATHERBY'S Studbooks.

TABLE OF COLOURS.

1 = black (bl.)
2 = black or brown (bl./br.).
3 = brown or black (br./bl.).
4 = brown (br.).
5 = brown or bay (br./b.).
6 = bay or brown (b./br.).
7 = bay (b.).
8 = bay or chestnut (b./ch.).
9 = chestnut or bay (ch./b.).
10 = chestnut (ch.).
11 = chestnut or roan (ch./ro.).
12 = roan or chestnut (ro./ch.).
13 = roan (ro.).
14 = roan or grey (ro./gr.).
15 = grey or roan (gr./ro.)
16 = grey (gr.).

TABLE I.—Direct Inheritance. First Generation.

Sires and Colts.

Sires.

Colts.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	3	0	0	7	0	0	12	0	0	7	0	0	0	0	0	0	29
2	bl./br.	0	0	0	2	0	1	4	0	0	0	0	0	0	0	0	0	7
3	br./bl.	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	4
4	br.	2	0	0	64	0	4	105	0	0	38	1	0	0	0	0	1	215
5	br./b.	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3
6	b./br.	0	0	0	12	0	0	23	0	0	8	0	0	0	0	0	1	44
7	b.	1	2	1	89	0	14	389	0	0	122	0	0	0	0	0	1	619
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
10	ch.	1	2	0	34	0	0	147	0	0	185	0	0	0	0	0	3	372
11	ch./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	0	0	0	3	0	0	2	0	0	0	0	0	0	5
Totals...	...	7	4	1	209	0	19	691	0	0	362	1	0	0	0	0	6	1300

TABLE II.—Direct Inheritance. First Generation.

Sires and Fillies.

Sires.

Fillies.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	0	0	0	3	0	0	10	0	0	3	0	0	0	0	0	0	16
2	bl./br.	0	0	0	8	0	0	3	0	0	1	0	0	0	0	0	0	12
3	br./bl.	0	0	0	1	0	0	6	0	0	0	0	0	0	0	0	0	7
4	br.	2	1	1	42	0	6	76	0	0	23	0	0	0	0	0	0	151
5	br./b.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
6	b./br.	0	0	0	6	0	0	29	0	0	7	0	0	0	0	0	0	42
7	b.	2	1	0	57	0	12	364	0	0	91	0	0	0	0	0	0	527
8	b./ch.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	2	1	0	21	0	1	118	0	0	133	2	0	0	0	0	1	279
11	ch./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	3
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
16	gr.	0	0	0	1	0	0	0	0	0	4	0	0	0	0	0	3	8
Totals…	…	6	3	1	139	0	19	610	0	0	264	2	0	0	0	0	6	1050

TABLE III.—Direct Inheritance. First Generation.

Dams and Colts.

Dams.

Colts.

		1 bl.	2 bl./br.	3 br./bl.	4 br.	5 br./b.	6 b./br.	7 b.	8 b./ch.	9 ch./b.	10 ch.	11 ch./ro.	12 ro./ch.	13 ro	14 ro./gr.	15 gr./ro.	16 gr.	Totals.
1	bl.	5	1	0	3	0	0	3	0	0	4	0	0	0	0	0	0	16
2	bl./br.	1	0	0	2	0	0	4	0	0	0	0	0	0	0	0	0	7
3	br./bl.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
4	br.	6	1	0	59	0	5	60	0	0	18	0	0	0	0	0	0	149
5	br./b.	0	0	0	3	0	0	1	0	0	1	0	0	0	0	0	0	5
6	b./br.	1	0	0	14	0	3	15	0	0	6	0	0	0	0	0	0	39
7	b.	9	1	0	76	0	6	295	0	1	86	0	1	1	0	0	4	480
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	6	0	0	27	0	2	127	0	0	133	0	0	2	0	0	3	300
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
16	gr.	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2
Totals...	...	28	3	1	184	0	16	505	0	1	249	1	1	4	0	0	7	1000

TABLE IV.—Direct Inheritance. First Generation.

Dams and Fillies.

Dams.

Fillies.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	1	1	0	1	0	1	4	0	0	2	0	0	0	0	0	0	10
2	bl./br.	1	0	0	4	0	0	8	0	0	2	0	0	0	0	0	0	15
3	br./bl.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
4	br.	3	0	0	52	0	2	67	0	0	18	0	0	1	0	0	0	143
5	br./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	b./br.	3	0	0	15	0	1	31	0	0	6	0	0	0	0	0	0	56
7	b.	13	1	0	74	0	6	288	1	0	79	0	0	1	0	0	1	464
8	b./ch.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	4	1	0	27	0	7	109	0	1	146	0	1	0	0	0	3	299
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
15	gr./ro.	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	2
16	gr.	0	0	0	1	0	0	1	0	0	2	0	0	0	0	0	3	7
Totals ...	...	25	3	0	175	0	18	509	1	1	256	0	1	4	0	0	7	1000

TABLE V.—Direct Inheritance. Second Generation.

Maternal Grandsires and Colts.

Grandsires.

Colts.

		1 bl.	2 bl./br.	3 br./bl.	4 br.	5 br./b.	6 b./br.	7 b.	8 b./ch.	9 ch./b.	10 ch.	11 ch./ro.	12 ro./ch.	13 ro.	14 ro./gr.	15 gr./ro.	16 gr.	Totals.
1	bl.	0	0	0	1	0	1	12	0	0	4	0	0	0	0	0	0	18
2	bl./br.	0	0	0	2	0	0	11	0	0	0	0	0	0	0	0	0	13
3	br./bl.	0	0	0	1	0	0	2	0	0	1	0	0	0	0	0	0	4
4	br.	1	0	0	29	0	2	94	0	0	29	0	0	0	0	0	1	156
5	br./b.	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	3
6	b./br.	2	0	0	7	0	3	24	0	0	12	0	0	0	0	0	0	48
7	b.	0	1	0	51	0	8	286	0	0	100	0	0	0	0	0	1	447
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	0	2	0	17	0	1	153	0	0	128	2	0	0	0	0	1	304
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
14	ro./gr.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	0	0	1	2	0	0	1	0	0	0	0	0	1	5
Totals...	...	3	3	0	110	0	16	587	0	0	275	2	0	0	0	0	4	1000

TABLE VI.—Direct Inheritance. Second Generation.

Maternal Grandsires and Fillies.

Grandsires.

Fillies.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	0	0	0	5	0	0	16	0	0	8	0	0	0	0	0	1	30
2	bl./br.	0	0	0	2	0	0	6	0	0	1	0	0	0	0	0	0	9
3	br./bl.	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	3
4	br.	0	2	0	22	0	4	72	0	0	31	0	0	0	0	0	0	131
5	br./b.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
6	b./br.	0	1	0	6	0	3	31	0	0	7	0	0	0	0	0	0	48
7	b.	1	3	0	55	0	5	305	0	0	101	0	0	0	0	0	0	470
8	b./ch.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	0	1	0	34	0	3	141	0	0	116	1	0	0	0	0	1	297
11	ch./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
16	gr.	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	2	6
Totals...	...	1	7	0	124	0	15	579	0	0	269	1	0	0	0	0	4	1000

TABLE VII.—Collateral Inheritance. First Degree. (Half-Brothers.)

Colts and Colts. Same Mare but different Sires.

First Colt.

Second Colt.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	2	1	0	6	0	1	8	0	0	5	0	0	0	0	0	0	23
2	bl./br.	0	0	0	2	0	0	5	0	0	6	0	0	0	0	0	0	13
3	br./bl.	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2
4	br.	4	3	0	44	0	10	72	0	0	34	0	0	0	0	1	0	168
5	br./b.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
6	b./br.	1	0	0	4	0	10	19	0	0	8	0	0	0	0	0	0	42
7	b.	5	3	2	62	1	19	242	0	0	119	0	0	0	0	0	1	454
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
10	ch.	2	2	0	24	0	5	119	0	0	134	0	0	0	0	0	0	286
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	1	0	0	2	0	0	3	0	0	0	0	0	2	8
Totals...	...	14	9	2	143	1	46	470	0	0	311	0	0	0	0	1	3	1000

TABLE VII$^{\text{bis}}$.—Collateral Heredity. First Degree. (Half-Brothers.)

Colts and Colts. Same Mare but different Sires.

Symmetrical Distribution.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	4	1	0	10	0	2	13	0	0	7	0	0	0	0	0	0	37
2	bl./br.	1	0	0	5	0	0	8	0	0	8	0	0	0	0	0	0	22
3	br./bl.	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	4
4	br.	10	5	0	88	0	14	134	0	0	58	0	0	0	0	1	1	311
5	br./b.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
6	b./br.	2	0	1	14	0	20	38	0	0	13	0	0	0	0	0	0	88
7	b.	13	8	3	134	1	38	484	0	1	238	0	0	1	0	0	3	924
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
10	ch.	7	8	0	58	1	13	238	0	0	268	0	0	1	0	0	3	597
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
16	gr.	0	0	0	1	0	0	3	0	0	3	0	0	0	0	0	4	11
Totals...	...	37	22	4	311	2	88	924	0	1	597	0	0	2	0	1	11	2000

TABLE VIII.—Collateral Heredity. First Degree. (Whole Brothers.)

Colts and Colts. Same Mare and Sire.

First Colt.

Second Colt.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	3	0	0	7	0	0	8	0	0	0	0	0	0	0	0	0	18
2	bl/br.	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	4
3	br./bl.	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2
4	br.	5	1	0	62	0	2	67	0	0	30	0	0	1	0	0	0	168
5	br./b.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
6	b./br.	0	0	0	14	0	2	17	0	0	3	0	0	0	0	0	0	36
7	b.	9	4	1	74	0	18	290	0	0	81	0	0	0	0	0	1	478
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	2	2	0	27	0	4	89	0	0	164	0	0	1	0	0	0	289
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
14	ro./gr.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
Totals...	...	20	7	2	188	1	26	473	0	0	278	0	0	2	0	0	3	1000

TABLE VIII$^{\text{bis}}$.—Collateral Heredity. First Degree. (Whole Brothers.)

Colts and Colts. Same Mare and Sire.

Symmetrical Distribution.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	6	0	1	12	0	0	17	0	0	2	0	0	0	0	0	0	38
2	bl./br.	0	0	1	4	0	0	4	0	0	2	0	0	0	0	0	0	11
3	br./bl.	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	4
4	br.	12	4	0	124	0	16	141	0	0	57	0	0	1	1	0	0	356
5	br./b.	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
6	b./br.	0	0	0	16	0	4	35	0	0	7	0	0	0	0	0	0	62
7	b.	17	4	2	141	0	35	580	0	0	170	0	0	1	0	0	1	951
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	2	2	0	57	0	7	170	0	0	328	0	0	1	0	0	0	567
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	3
14	ro./gr.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	5
Totals...	...	38	11	4	356	2	62	951	0	0	567	0	0	3	1	0	5	2000

Table IX.—Collateral Heredity. (Half Sisters.)

Fillies and Fillies. Same Mare but different Sire

First Filly.

Second Filly.		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	2	0	0	4	0	1	13	0	0	4	0	0	0	0	0	0	24
2	bl./br.	0	0	0	1	0	0	3	0	0	3	0	0	0	0	0	1	8
3	br./bl.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
4	br.	4	1	0	42	0	5	64	0	0	25	0	0	0	0	0	0	141
5	br./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	b./br.	0	1	0	3	0	6	23	0	0	7	0	0	0	0	0	0	40
7	b.	9	3	1	61	0	21	313	0	0	103	0	0	0	0	0	2	513
8	b./ch.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	5	5	0	26	0	10	91	0	0	119	0	0	0	0	1	1	258
11	ch./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	4
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2
16	gr.	0	0	0	3	0	0	2	0	0	1	0	0	0	0	0	1	7
Totals...	...	20	10	1	140	0	44	513	0	0	266	0	0	0	0	1	5	1000

TABLE IX$^{\text{bis}}$.—Collateral Heredity. First Degree. (Half-Sisters.)

Fillies and Fillies. Same Mare but different Sires.

Symmetrical Distribution.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	4	0	0	8	0	1	22	0	0	9	0	0	0	0	0	0	44
2	bl./br.	0	0	0	2	0	1	6	0	0	8	0	0	0	0	0	1	18
3	br./bl.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
4	br.	8	2	0	84	0	8	125	0	0	51	0	0	0	0	0	3	281
5	br./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	b./br.	1	1	0	8	0	12	44	0	0	17	0	0	0	0	1	0	84
7	b.	22	6	1	125	0	44	626	0	0	194	1	0	2	0	1	4	1026
8	b./ch.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	9	8	1	51	0	17	194	1	0	238	0	0	2	0	1	2	524
11	ch./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	4
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	3
16	gr.	0	1	0	3	0	0	4	0	0	2	0	0	0	0	0	2	12
Totals...	...	44	18	2	281	0	84	1026	1	0	524	1	0	4	0	3	12	2000

TABLE X.—Collateral Heredity. First Degree. (Whole Sisters.)

Fillies and Fillies. Same Mare and same Sire.

First Filly.

Second Filly.

		1. bl.	2. bl./br.	3. br./bl.	4 br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	6	1	0	6	0	1	11	0	0	4	0	0	0	0	0	0	29
2	bl./br.	1	0	0	2	0	2	3	0	0	0	0	0	0	0	0	0	8
3	br./bl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	br.	6	5	0	64	0	4	53	0	0	21	0	0	0	0	0	0	153
5	br./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	b./br.	1	1	0	5	0	4	18	0	0	3	0	0	0	0	0	0	32
7	b.	8	2	0	55	0	17	336	0	0	77	0	0	0	0	0	1	496
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	4	1	0	23	0	3	77	0	0	168	0	1	0	0	0	0	277
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	4	5
Totals...	...	26	10	0	155	0	31	499	0	0	273	0	1	0	0	0	5	1000

TABLE X$^{\text{bis}}$.—Collateral Heredity. First Degree. (Whole Sisters).

Fillies and Fillies. Same Mare and same Sire.

Symmetrical Distribution.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	12	2	0	12	0	2	19	0	0	8	0	0	0	0	0	0	55
2	bl./br.	2	0	0	7	0	3	5	0	0	1	0	0	0	0	0	0	18
3	br./bl.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	br.	12	7	0	128	0	9	108	0	0	44	0	0	0	0	0	0	308
5	br./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	b./br.	2	3	0	9	0	8	35	0	0	6	0	0	0	0	0	0	63
7	b.	19	5	0	108	0	35	672	0	0	154	0	0	0	0	0	2	995
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	8	1	0	44	0	6	154	0	0	336	0	1	0	0	0	0	550
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
13	ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	8	10
Totals...	...	55	18	0	308	0	63	995	0	0	550	0	1	0	0	0	10	2000

TABLE XI.—Collateral Heredity. First Degree. (Half Sister and Half Brother.)

Fillies and Colts. Same Mare but different Sires.

Fillies.

Colts.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	0	0	0	4	0	0	7	0	0	7	0	0	0	0	0	0	18
2	bl./br.	1	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0	5
3	br./bl.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
4	br.	3	0	0	34	0	8	71	0	0	32	0	0	1	0	1	0	150
5	br./b.	0	1	0	2	0	1	0	0	0	1	0	0	0	0	0	0	5
6	b./br.	0	0	0	13	0	10	18	0	0	5	0	0	0	0	0	1	47
7	b.	5	8	0	61	0	22	263	0	0	112	0	0	3	0	0	2	476
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	4	2	0	28	0	15	125	0	0	116	0	0	1	0	1	0	292
11	ch./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
16	gr.	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	3
Totals...	...	13	11	0	145	0	57	489	0	0	274	0	0	5	0	2	4	1000

TABLE XII.—Collateral Heredity, First Degree. (Whole Brother and Whole Sister.)

Fillies and Colts. Same Mare and Sire.

Fillies.

Colts.

		1. bl.	2. bl./br.	3. br./bl.	4. br.	5. br./b.	6. b./br.	7. b.	8. b./ch.	9. ch./b.	10. ch.	11. ch./ro.	12. ro./ch.	13. ro.	14. ro./gr.	15. gr./ro.	16. gr.	Totals.
1	bl.	6	0	0	5	0	0	6	0	0	3	0	0	0	0	0	0	20
2	bl./br.	0	2	0	0	0	0	1	0	0	1	0	0	0	0	0	0	4
3	br./bl.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
4	br.	3	1	0	63	0	9	69	0	0	22	0	0	0	0	1	0	168
5	br./b.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
6	br./b.	1	0	0	5	0	3	11	0	0	6	0	0	0	0	0	0	26
7	b.	8	5	0	63	0	12	332	0	0	77	0	0	0	0	0	2	499
8	b./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	ch./b.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	ch.	1	1	0	26	0	4	97	0	0	141	0	0	1	0	0	0	271
11	ch./ro.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
12	ro./ch.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	ro./gr.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	gr./ro.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	gr.	0	1	0	0	0	2	2	0	0	2	0	0	0	0	0	2	9
Totals ...	...	20	10	0	162	0	30	520	0	0	252	0	0	1	0	1	4	1000

APPENDIX II.

Tables of Eye-colour Inheritance in Man, extracted by KARL PEARSON from Mr. FRANCIS GALTON'S Family Records.

TABLE OF TINTS.

1 = light blue.
2 = blue, dark blue.
3 = blue-green, grey.
4 = dark grey, hazel.
5 = light brown.
6 = brown.
7 = dark brown.
8 = very dark brown, black.

This grouping is not quite in keeping with more recent divisions of eye-colour, but being that adopted by Mr. GALTON in his original collection of data, it could not be modified in accordance with present practice.

TABLES for the Direct Inheritance of Eye-colour. First Generation.

I.—Fathers and Sons. 1000 Cases.

Fathers.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Sons.	1	9	12	5	5	0	1	2	0	34
	2	10	163	65	36	1	7	15	4	301
	3	10	73	124	41	1	12	18	5	284
	4	4	21	34	55	0	11	11	1	137
	5	0	0	0	0	2	2	1	0	5
	6	1	26	12	19	1	19	16	6	100
	7	1	23	16	14	0	11	31	2	98
	8	1	4	8	10	0	1	7	10	41
	Totals	36	322	264	180	5	64	101	28	1000

II.—Fathers and Daughters. 1000 Cases.

Fathers.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Daughters.	1	4	9	11	4	0	1	2	1	32
	2	11	139	57	31	0	6	24	5	273
	3	9	73	111	38	1	15	19	3	269
	4	5	43	34	54	2	10	14	3	165
	5	0	1	3	0	0	3	1	0	8
	6	1	45	13	19	0	23	15	3	119
	7	2	27	10	12	0	7	41	6	105
	8	0	8	4	0	0	2	11	4	29
	Totals	32	345	243	158	3	67	127	25	1000

III.—Mothers and Sons. 1000 Cases.

Mothers.

Sons.

Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	5	14	6	3	0	1	0	6	35
2	12	119	83	29	8	20	21	9	301
3	13	54	113	35	4	37	14	8	278
4	3	21	26	54	1	17	6	6	134
5	0	1	1	0	0	3	0	0	5
6	1	9	26	10	1	30	24	3	104
7	1	9	19	16	0	18	31	7	101
8	0	7	15	4	1	3	5	7	42
Totals	35	234	289	151	15	129	101	46	1000

IV.—Mothers and Daughters. 1000 Cases.

Mothers.

Daughters.

Tints.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	5	15	3	2	2	2	2	0	31
2	7	99	67	29	2	15	23	13	255
3	7	77	111	38	1	26	14	6	280
4	5	22	34	46	2	27	21	7	164
5	0	2	2	0	3	1	2	1	11
6	0	13	27	20	1	35	17	7	120
7	0	13	21	16	1	19	26	9	105
8	1	5	7	2	1	4	12	2	34
Totals.	25	246	272	153	13	129	117	45	1000

TABLES for the Collateral Inheritance of Eye-colour.

V^a.—Brothers and Brothers. 1500 Cases.

First Brother.

Second Brother.

First.	1.	2.	3.	4.	5.	6.	7	8.	Totals.
1	8	2	3	4	0	0	0	0	19
2	36	202	23	17	0	6	4	3	291
3	16	182	209	26	0	4	2	2	441
4	6	36	71	84	0	7	2	0	206
5	0	3	2	1	0	1	0	0	7
6	3	56	50	39	0	34	5	6	193
7	6	37	76	48	1	36	36	2	242
8	4	24	26	18	0	8	6	15	101
Totals	79	542	460	237	1	96	55	30	1500

VI^{a}.—Sisters and Sisters. 1500 Cases.

First Sister.

Second Sister.

First.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	10	2	1	1	0	0	0	0	14
2	17	147	29	6	0	10	6	2	217
3	10	136	186	24	0	9	5	3	373
4	3	75	94	66	0	1	10	0	249
5	0	3	5	2	2	0	1	0	13
6	2	57	69	55	5	52	9	2	251
7	4	56	61	52	10	59	49	0	291
8	2	20	10	7	6	13	26	8	92
Totals	48	496	455	213	23	144	106	15	1500

V^{b}.—Brothers and Brothers. Symmetrical System.

Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	16	38	19	10	0	3	6	6	98
2	38	404	205	53	3	62	41	27	833
3	19	205	418	97	2	54	78	28	901
4	10	53	97	168	1	46	50	18	443
5	0	3	2	1	0	1	1	0	8
6	3	62	54	46	1	68	41	14	289
7	6	41	78	50	1	41	72	8	297
8	6	27	28	18	0	14	8	30	131
Totals	98	833	901	443	8	289	297	131	3000

VI^{b}.—Sisters and Sisters. Symmetrical System.

Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	20	19	11	4	0	2	4	2	62
2	19	294	165	81	3	67	62	22	713
3	11	165	372	118	5	78	66	13	828
4	4	81	118	132	2	56	62	7	462
5	0	3	5	2	4	5	11	6	36
6	2	67	78	56	5	104	68	15	395
7	4	62	66	62	11	68	98	26	397
8	2	22	13	7	6	15	26	16	107
Totals	62	713	828	462	36	395	397	107	3000

VII.—Brothers and Sisters. 1500 Cases.

Brothers.

Sisters.

Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	5	9	18	4	0	0	1	0	37
2	20	163	101	36	0	28	19	13	380
3	9	98	193	50	0	37	17	14	418
4	5	36	49	67	3	28	13	16	217
5	0	2	5	1	1	2	2	3	16
6	3	47	41	27	4	42	17	14	195
7	4	34	49	22	3	27	30	19	178
8	1	10	7	1	0	10	8	22	59
Totals	47	399	463	208	11	174	107	91	1500

TABLE for Assortative Mating in Eye-colour.

VIII.—Husbands and Wives. 774 Cases.

Husbands.

Wives.

Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	2	13	4	3	0	1	2	0	25
2	6	87	42	26	0	16	13	6	196
3	6	56	93	31	1	16	11	6	220
4	4	32	35	18	1	15	6	1	112
5	0	0	5	1	0	0	1	0	7
6	2	38	27	10	1	12	10	1	101
7	5	20	28	7	1	6	12	4	83
8	2	8	8	2	0	2	4	4	30
Totals	27	254	242	98	4	68	59	22	774

TABLES for the Direct Inheritance of Eye-colour. Second Generation.

IX.—Paternal Grandfather and Grandson. 765 Cases.

Paternal Grandfather.

Grandson.

First.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
1	4	10	3	0	0	1	3	0	21
2	7	115	31	20	1	6	13	3	196
3	5	64	109	21	0	10	22	4	235
4	2	25	40	21	0	9	13	6	116
5	0	0	0	1	0	1	0	0	2
6	0	14	32	11	0	15	5	2	79
7	4	16	16	9	1	11	21	2	80
8	0	6	5	0	0	3	16	6	36
Totals	22	250	236	83	2	56	93	23	765

X.—Paternal Grandfather and Granddaughter. 681 Cases.

Paternal Grandfather.

	First.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Granddaughter.	1	3	6	4	5	0	1	1	0	20
	2	2	94	32	10	2	6	16	4	166
	3	5	67	71	17	0	9	20	3	192
	4	4	35	33	26	1	10	9	3	121
	5	0	3	4	1	0	1	2	1	12
	6	1	16	21	11	0	15	6	4	74
	7	3	10	20	11	1	8	15	3	71
	8	0	2	5	1	1	1	10	5	25
	Totals	18	233	190	82	5	51	79	23	681

TABLE XI.—Maternal Grandfather and Grandson. 771 Cases.

Maternal Grandfather.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Grandson.	1	3	11	3	1	—	—	1	—	19
	2	8	113	46	22	1	13	5	3	211
	3	10	87	89	12	—	11	8	3	220
	4	4	33	35	22	—	15	6	2	117
	5	—	1	1	—	—	—	—	—	2
	6	2	25	25	7	—	14	7	4	84
	7	1	22	26	6	2	9	10	4	80
	8	—	12	12	6	—	4	3	1	38
	Totals	28	304	237	76	3	66	40	17	771

TABLE XII.—Maternal Grandfather and Granddaughter. 687 Cases.

Maternal Grandfather.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Granddaughter.	1	1	3	7	2	—	—	1	—	14
	2	8	84	35	11	—	13	6	2	159
	3	11	67	76	18	—	7	15	5	199
	4	7	41	40	14	—	15	11	5	133
	5	—	5	2	—	—	2	1	—	10
	6	4	21	32	1	—	16	5	2	81
	7	4	15	14	8	1	7	19	2	70
	8	—	5	5	1	—	1	5	4	21
	Totals	35	241	211	55	1	61	63	20	687

TABLE XIII.—Paternal Grandfather and Grandson. 741 Cases.

Paternal Grandmother.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Grandson.	1	1	2	7	1	1	2	3	—	17
	2	6	62	69	22	4	15	25	4	207
	3	4	31	95	22	1	25	33	9	220
	4	3	18	36	20	4	15	16	4	116
	5	—	—	—	1	—	—	1	1	3
	6	1	10	23	6	2	16	10	4	72
	7	3	15	10	4	1	14	13	11	71
	8	1	10	3	3	—	5	5	8	35
	Totals	19	148	243	79	13	92	106	41	741

TABLE XIV.—Paternal Grandmother and Granddaughter. 717 Cases.

Paternal Grandmother.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Granddaughter.	1	—	3	3	2	—	—	6	2	16
	2	7	53	56	14	2	13	28	8	181
	3	8	35	65	22	6	29	28	7	200
	4	4	29	36	20	3	16	23	8	139
	5	1	—	3	1	—	5	1	—	11
	6	—	9	29	2	4	27	8	3	82
	7	—	10	15	12	2	10	12	7	68
	8	1	2	1	2	1	4	4	5	20
	Totals	21	141	208	75	18	104	110	40	717

TABLE XV.—Maternal Grandmother and Grandson. 756 Cases.

Maternal Grandmother.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Grandson.	1	1	10	1	3	—	—	3	1	19
	2	10	68	53	23	—	24	13	13	204
	3	9	39	67	38	—	32	23	11	219
	4	3	34	19	30	—	19	8	4	117
	5	—	—	1	1	—	—	—	—	2
	6	—	20	11	10	—	24	18	1	84
	7	2	9	23	11	1	17	17	—	80
	8	—	4	6	5	—	6	3	7	31
	Totals	25	184	181	121	1	122	85	37	756

Table XVI.—Maternal Grandmother and Granddaughter. 739 Cases.

Maternal Grandmother.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Granddaughter.	1	2	16	—	—	—	—	—	—	18
	2	7	66	34	13	—	21	15	6	162
	3	12	62	55	25	1	27	23	5	210
	4	6	32	36	25	—	23	15	7	144
	5	—	1	3	2	—	3	3	—	12
	6	1	14	21	11	—	27	17	2	93
	7	—	19	17	7	—	16	17	3	76
	8	—	5	4	2	—	7	3	3	24
	Totals	28	212	170	85	1	124	93	26	739

Tables for the Collateral Inheritance of Eye-colour. Second Degree.

XVII.—Paternal Uncle and Nephew. 1290 Cases.

Paternal Uncle.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Total.
Nephew.	1	4	10	11	6	1	4	5	2	43
	2	11	136	98	40	0	26	48	12	371
	3	8	84	157	26	1	27	54	7	364
	4	0	29	69	36	1	19	27	12	193
	5	0	2	1	0	0	2	1	0	6
	6	1	31	35	7	1	30	19	3	127
	7	2	21	27	24	1	13	34	11	133
	8	0	11	7	6	0	10	8	11	53
	Total	26	324	405	145	5	131	196	58	1290

XVIII.—Paternal Uncle and Niece. 1128 Cases.

Paternal Uncle.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Total.
Niece.	1	2	10	6	2	0	1	6	2	29
	2	7	85	61	27	0	29	26	13	248
	3	5	82	126	29	1	26	43	7	319
	4	2	47	73	40	1	29	40	5	237
	5	1	8	1	4	0	1	5	4	24
	6	1	26	35	12	1	8	42	3	128
	7	1	20	25	19	0	22	26	7	120
	8	0	4	2	3	0	5	3	6	23
	Total	26	282	329	136	3	121	191	47	1128

TABLE XIX.—Maternal Uncle and Nephew. 1242 Cases.

Maternal Uncle.

	Tint.	1.	2.	3.	4.	5.	6.	7	8.	Totals.
Nephew.	1	1	8	13	3	0	3	4	1	33
	2	17	137	71	29	0	19	14	9	296
	3	10	128	153	26	0	29	34	3	383
	4	2	50	62	28	0	22	14	1	179
	5	0	1	0	0	0	0	1	0	2
	6	4	33	29	12	0	35	20	3	136
	7	1	33	40	11	0	26	27	2	140
	8	0	9	17	23	0	8	3	13	73
	Totals	35	399	385	132	0	142	117	32	1242

TABLE XX.—Maternal Uncle and Niece. 1434 Cases.

Maternal Uncle.

	Tint.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Niece.	1	2	15	9	2	0	2	1	0	31
	2	6	99	76	23	0	18	13	11	246
	3	18	100	108	23	0	37	36	10	332
	4	4	72	64	28	0	16	21	9	214
	5	0	14	2	3	0	8	5	0	32
	6	5	38	41	10	0	23	11	4	132
	7	1	27	25	7	0	19	14	3	96
	8	0	15	5	6	0	9	11	5	51
	Totals	36	380	330	102	0	132	112	42	1134

TABLE XXI.—Paternal Aunt and Nephew. 1186 Cases.

Paternal Aunt.

	Tints.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Nephew.	1	6	13	5	3	1	4	6	4	42
	2	19	113	83	45	—	36	29	5	330
	3	10	81	147	30	—	29	35	8	340
	4	8	28	66	38	—	18	22	11	191
	5	—	—	—	—	—	—	—	—	0
	6	3	23	35	12	1	35	10	5	124
	7	5	22	28	19	—	18	15	5	112
	8	1	4	9	8	—	6	4	13	47
	Totals	52	284	373	155	2	148	121	51	1186

Table XXII.—Paternal Aunt and Niece. 1149 Cases.

Paternal Aunt.

	Tints.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Niece.	1	2	11	2	3	—	2	11	2	33
	2	15	89	62	37	2	25	40	14	284
	3	12	93	119	40	3	41	26	12	346
	4	10	36	62	43	5	25	21	11	213
	5	—	5	7	—	—	1	3	—	16
	6	1	24	33	16	1	29	19	5	128
	7	2	20	28	12	2	10	22	4	100
	8	—	7	—	4	—	5	9	4	29
	Totals	42	285	313	155	13	138	151	52	1149

Table XXIII.—Maternal Aunt and Nephew. 1145 Cases.

Maternal Aunt.

	First.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Nephew.	1	4	8	7	3	—	2	3	1	28
	2	5	117	81	29	—	43	29	6	310
	3	1	73	132	38	—	57	43	3	347
	4	1	20	54	27	1	21	11	—	135
	5	—	—	3	2	—	1	—	—	6
	6	—	24	35	22	—	30	23	3	137
	7	—	26	29	20	1	26	25	8	135
	8	—	14	5	10	—	12	4	2	47
	Totals	11	282	346	151	2	192	138	23	1145

Table XXIV.—Maternal Aunt and Niece. 1058 Cases.

Maternal Aunt.

	First.	1.	2.	3.	4.	5.	6.	7.	8.	Totals.
Niece.	1	2	3	10	—	—	—	—	—	15
	1	5	87	86	31	—	23	14	12	258
	3	3	71	125	32	1	49	41	3	325
	4	—	39	51	31	1	33	19	6	180
	5	—	4	6	1	—	8	5	3	27
	6	1	25	47	10	—	24	9	2	118
	7	—	30	29	11	—	14	18	10	112
	8	—	5	4	5	—	2	4	3	23
	Totals	11	264	358	121	2	153	110	39	1058

[Notes added July 3, 1900.

Note I. *Inheritance of Temper and Artistic Instinct.*—In additional to the fraternal correlations given on p. 102, I have dealt with Mr. GALTON's statistics for the inheritance of good and bad temper given in his 'Natural Inheritance' (p. 235). The following gives the distribution of good and bad temper among 1,294 brethren, as deduced by Mr. YULE.

First Brother.

		Good Temper.	Bad Temper.	Totals.
Second Brother.	Good temper.	330	255	585
	Bad temper.	255	454	709
	Totals	585	709	1294

The correlation is ·3167.

A like table is that for artistic instinct in the direct line:—

Parentage.

		Artistic.	Non-artistic.	Totals.
Child.	Artistic.	296	173	469
	Non-artistic.	372	666	1038
	Totals	668	839	1507

In this case the correlation is ·4039.

The fraternal correlation is somewhat low. The exact significance of the parental correlation is also somewhat vague, as the parentage is classified as artistic when *one* or *both* parents are artistic. But the two tables are very suggestive, they indicate how the new method will enable us to deal quantitatively even with characters like temper and artistic instinct to which it is impossible to apply directly a quantitative scale. With the introduction of a third or medium class, I believe it will be possible to obtain excellent results for heredity from very simple observations, and I have in hand at the present time a large series of observations on collateral heredity based upon such simple classifications. The reader should further consult

Mr. G. U. YULE's remarks on the association of temper and of artistic instinct in his memoir on "Association," 'Phil. Trans.,' A, vol. 194, p. 290, 1900.

Note II. *On the Correlation of Fertility and Eye-Colour.*—In the course of the present paper I have frequently referred to a probable influence of reproductive selection as the source of the progressive change in eye-colour, *i.e.*, to a possibility that eye-colour is correlated with fertility. I saw from Mr. GALTON's tables that in many cases the whole family had not been recorded, probably the eye-colour of the dead or of absentees being unknown. It appeared to me accordingly that it would be impossible to deal directly with the problem of fertility. However, it has since occurred to me that there is nothing likely to give the missing members of families a bias towards one rather than another eye-colour, and that we may simply treat them as a purely random subtraction from the total results. Assuming this, Mr. L. N. FILON, M.A., has prepared for me tables of father's and mother's eye-colour and of the recorded number of their children. From these* I take first the following results, premising (i.) that I call "light eyed," persons with eye-colours 1, 2 and 3, and "dark eyed," persons with eye-colours 4, 5, 6, 7, 8, *i.e.*, drawing the line between light and dark grey; (ii.) that I take as small families those with 0, 1, 2, or 3, recorded children and as large those with 4 or more recorded children.

Father.

		Light Eyed.	Dark Eyed.	Totals.
Family.	Small.	313	141	454
	Large.	264	139	403
	Totals	577	280	857

Mother

		Light Eyed.	Dark Eyed.	Totals.
Family.	Small.	253	202	455
	Large.	225	169	394
	Totals	478	371	849

---

* Correlation tables were prepared of the size of families 0 to 15, and of the eye-colours 1 to 8, but it does not seem needful to print them *in extenso*.

We have, accordingly, by the method of the present memoir :—

Correlation of size of family with darkness of eye-colour

$$= \quad \cdot 0595, \text{ for fathers.}$$
$$= - \cdot 0239, \text{ for mothers.}$$

The former is just sensible, the latter hardly sensible relative to the probable error. So far as they can be relied upon, they would denote that fathers have more children the darker eyed they are, and mothers more children the lighter eyed they are. This is in accordance with the result given in the memoir, that the modern generation is darker than its male and lighter than its female ancestry, but it is not the explanation given in the text, although it is probably the true one. If it be the true one, dark fathers and light mothers ought to present the most fertile unions, and it seemed desirable to test this directly. We have already seen that there exists an assortative mating in eye-colour, like tending to mate with like, the co-efficient of correlation being about ·1 ; hence if we were to correlate the eye-colour of mothers and fathers, *i.e.*, husbands and wives weighted with their fertility, we ought to find this result substantially reduced. The following is the table :—

Fathers.

Mothers.		Light Eyed.	Dark Eyed.	Totals.
	Light Eyed.	1183	612	1795
	Dark Eyed.	826	455	1281
	Totals	2009	1067	3076

We find $r = \cdot 0239$, or the correlation has been reduced to a fifth of its previous value, and is now of the order of its probable error. To mark still further this increased fertility of heterogamous unions, I add two further tables, giving the mean number of recorded offspring for various classifications of parental eye-colour.

Fathers.

Mothers.	Colours 1–3.	Colours 4–8.	Average of totals.
Colours 1–3.	3·83	4·57	4·07
Colours 4–8.	3·82	3·73	3·79
Average of totals	3·83	4·17	3·94

Fathers.

Mothers.	Colours 1–2.	Colours 3–8.	Average of totals
Colours 1–2.	3·19	4·52	3·86
Colours 3–8.	3·98	3·96	3·97
Average of totals	3·68	4·09	3·94

The first table entirely confirms all the conclusions reached,—dark fathers and light mothers are most fertile absolutely and in union. The second table shows that it is the blue-green and grey rather than pure blue-eyed mothers who are most fertile. This supplementary investigation accordingly seems to support the view of the text of the memoir, namely that reproductive selection is the source of the secular change in eye-colour noted, only the prepotent fertility which is replacing the blue-eyed element is in the first place that of the dark-eyed male, and only in the second place due to mothers having eye-colours dark or light other than true blue. We seem accordingly in eye-colour to have reproductive selection working through heterogamy rather than through homogamy as in the case of stature.* The effect, however, is like,—the progressive elimination of one type of character.]

---

* See 'Roy. Soc. Proc.,' vol. 66, p. 30, and vol. 66, p. 316 *et seq.*