

If we compare the two sexes, we see that except in the matter of stature the married woman is *relatively* as variable as the married man, while in all three characters the young woman is relatively more variable than the young man. The supposed preponderance of male variability is thus again very fully negated, for large statistics of typical physical characters in mankind*.

Turning to the correlations we see (*a*) that in the older generation the mother is less highly correlated than the father, (*b*) that in the younger generation the son is less highly correlated than the daughter, (*c*) that the younger generation of both sexes is more highly correlated than the older generation. Now the effect of selection is to reduce correlation, hence if selection—a selective death-rate—be a real factor in the case of man and we know it to be so, we should certainly expect the correlations between the ages of youth and of middle life to be reduced. They are thus reduced, but far more markedly so in the case of woman than in that of man. Now as far as our data at present reach we know that the male baby is more variable and more highly correlated than the female†. In youth the woman is more variable and more highly correlated than the man; in adult age after child-bearing she is less highly correlated and perhaps very slightly less variable. It would thus seem that between birth and manhood the male is selected and falls in both variability and correlation below his sister. With womanhood comes her period of selection, sexual selection for wifeness, natural and reproductive selection for motherhood. These act with a little expected intensity and leave mothers of adult families with far less variability and correlation than their husbands have.

Of course these changes in variability and correlation may be partly growth changes, but since on the average the man reaches his maximum size four or five years later than the woman and at least four or five years beyond the average age of our group sons, it is difficult to account for the wide difference in variation and correlation between daughters and mothers as compared with that between sons and fathers by growth changes only.

I am inclined to think Table I. is very illustrative of the nature of selection among mankind, and further that it is also hopeful, not as regards the quantity, of which it takes no account, but as regards the quality of the offspring of a fair sample of the English middle classes.

(v) *Direct Assortative Mating in Man.*

We have seen above that all women, if they indeed become wives, do not become the mothers of adult children, i.e. the mothers of the second generation are not a random sample of their own generation. However it may arise there is

* See *The Chances of Death*, Vol. I. pp. 256—377. A recent criticism by Mr Havelock Ellis of my view that there is no preponderating variability of man over woman seems to need no reply, for the author does not appear to understand what weight is to be given to scientific evidence as compared with vague generalities.

† *R. S. Proc.* Vol. 66, p. 25.

certainly a "preferential mating"* taking place. I think we may safely assert that the first factor of sexual selection is active in man. I now turn to the second factor, "assortative mating." If certain women are rejected, at any rate as mothers of adult children, do the remainder mate at random as far as the above three characters are concerned? The answer is most decidedly in the negative, there is a very sensible resemblance in size between husband and wife, which *à priori* I should have said was hardly conceivable. Table II, gives the direct and cross coefficients for assortative mating in man.

TABLE II.

Assortative Mating. Based on 1000 to 1050 Cases of Husband and Wife.

	Husband's Character	Wife's Character	Correlation and Probable Error	Symbol
Direct	Stature	Stature	$\cdot 2804 \pm \cdot 0189$	r_{12}
	Span	Span	$\cdot 1989 \pm \cdot 0204$	r_{36}
	Forearm	Forearm	$\cdot 1977 \pm \cdot 0205$	r_{56}
Cross	Stature	Span	$\cdot 1820 \pm \cdot 0201$	r_{14}
	Stature	Forearm	$\cdot 1403 \pm \cdot 0204$	r_{16}
	Span	Stature	$\cdot 2023 \pm \cdot 0199$	r_{32}
	Span	Forearm	$\cdot 1533 \pm \cdot 0203$	r_{36}
	Forearm	Stature	$\cdot 1784 \pm \cdot 0201$	r_{52}
	Forearm	Span	$\cdot 1545 \pm \cdot 0203$	r_{54}

We see at once that between the same physical characters in the husband and wife of adult children there is a correlation of upwards of $\cdot 2$, a most remarkable degree of resemblance, greater than that of great-grandparents to their great-grandchildren (about $\cdot 19$ †), and probably greater than that of first cousins to each other. We could hardly want stronger evidence of the existence of assortative mating in man, i.e. of the actuality of sexual selection. I had previously found‡ from Mr Galton's *Family Records*, that the correlation in stature between *husband and wife* was $\cdot 09 \pm \cdot 05$, but between *father and mother* of adult offspring was $\cdot 18 \pm \cdot 02$. Considering the comparative smallness of material, the latter result is in very good agreement with the present, but it seems to indicate that a portion of the observed resemblance in the parents of adult offspring is due to reproductive selection, i.e. homogamy being a factor of fertility. If the parents of adult children are on the average more alike than first cousins, then it follows that any evils which may flow from first cousin marriage depend not on likeness of characters, but on sameness of stock§.

That the whole result, further, is not due to a mere general custom of men and women mating with persons not differing widely from them in *stature*, is

* *Phil. Trans.* Vol. 187, p. 253 *et seq.* See especially p. 258.

† *Biometrika*, Vol. II, p. 221.

‡ *R. S. Proc.* Vol. 66, p. 30.

§ I have discussed this point more at length, *R. S. Proc.* Vol. 66, p. 29.

shown by the sensible correlation there is in eye-colour between husband and wife, i.e. $10 \pm 04^*$, which is closely in agreement with the results for stature of husband and wife from the same data.

We may, however, estimate how far mating with regard to stature would produce resemblances in span and forearm. Let the subscripts 1, 3, 5 refer to three organs in a male of the population who marries, and 2, 4, 6 to the corresponding organs of a female of the marrying part of the population. Then $r_{13}, r_{35}, r_{51}, r_{24}, r_{46}, r_{62}$ are organic correlations such as we have tabled on p. 370. All correlations such as $r_{12}, r_{14}, r_{16}, r_{22}, r_{34}, r_{36}, r_{52}, r_{54}, r_{56}$ are zero, if we mated pairs at random. Now let them be assortatively mated and let $\rho_{12}, \rho_{34}, \rho_{56}$ represent the degree of resemblance in the sexual selection. Let r_{12}, r_{34}, r_{56} be the apparent correlations of mated pairs; then r_{12} will not be equal to ρ_{12} , for it is partly due to the degree of assortative mating indicated in ρ_{34} and ρ_{56} , because 3 and 5 are organically correlated with 1, and 4 and 6 with 2; thus the selection of 3's and 5's to associate with 4's and 6's would indirectly influence the relationship of 1 and 2, even if there were no direct associating of 1's and 2's. The relationship of r_{12}, r_{34}, r_{56} to $\rho_{12}, \rho_{34}, \rho_{56}$ may be easily found from my memoir on the influence of selection on variability and correlation†. We have only to put in the formulæ of pp. 15—17 the appropriate values for the population described above and we find:

$$\left. \begin{aligned} r_{12} &= \rho_{12} && + \rho_{34} r_{13} r_{24} + \rho_{56} r_{15} r_{26} \\ r_{34} &= \rho_{12} r_{13} r_{24} + \rho_{34} && + \rho_{56} r_{35} r_{46} \\ r_{56} &= \rho_{12} r_{15} r_{26} + \rho_{34} r_{35} r_{46} + \rho_{56} \end{aligned} \right\} \dots\dots\dots (i).$$

Now suppose that 1 and 2 represent statures, 3 and 4 spans, and 5 and 6 forearms. Then if all assortative mating be due to selection of stature, we might put ρ_{34} and ρ_{56} zero above and we should have:

$$\rho_{12} = r_{12}, \quad r_{34} = r_{12} r_{13} r_{24}, \quad r_{56} = r_{12} r_{15} r_{26}.$$

But $r_{13} = \cdot7829, r_{24} = \cdot7560, r_{15} = \cdot6397, r_{26} = \cdot5968,$ and $r_{12} = \cdot2804$. This leads to

$$r_{34} = \cdot1660 \text{ and } r_{56} = \cdot1071,$$

as against the observed values:

$$r_{34} = \cdot1989 \text{ and } r_{56} = \cdot1977.$$

The former values are too small in both cases and, I think, we may safely assert, that the likeness of husband and wife in forearm and span is not *solely* due to a selection of stature.

Another explanation of these high coefficients of assortative mating has been suggested to me, namely that the population of England is built up of a number

* *Phil. Trans.* Vol. 195, A, p. 113. See also pp. 148—150, where it is shown that heterogamy rather than homogamy in eye-colour tends to increased fertility. If this be confirmed, eye-colour differs much in effect from stature.

† *Phil. Trans.* Vol. 200, p. 1 *et seq.*

of local races, and that men and women mate within their locality. Now it appears to me that this argument would be far more valid, if my material was drawn in bulk from local lower middle and artizan classes. But it is very doubtful how far it is true of the middle classes, such as provide the students at the London colleges. The middle classes undoubtedly marry in their own "sets," but these are hardly local sets. Further, a wide series of assortative mating observations have been made on another, wholly different class of characters, in which local race is regarded, and the coefficients come out as high as in the present data. Hence, I think, we are forced to the conclusion that the bulk of the observed resemblance in physical characters between parents is due to a direct, if quite unconscious, selection of like by like, and possibly in a contributory degree to a likeness in parents for the characters under consideration emphasising their fertility.

The amount of "consciousness" in the selection may possibly be measured by the difference between the stature-stature correlation and those for span-span, and forearm-forearm.

(vi) *Cross-Assortative Mating in Man.*

The second part of Table II. gives the cross-coefficients, for example, the correlation between husband's stature and wife's forearm. We might *à priori*, perhaps, anticipate that the correlation between a first organ in the husband and a second in the wife, would be equal to the correlation between the second in the husband and the first in the wife. This is actually the case for span and forearm, and, perhaps, we may consider for stature and span; the results for stature and forearm are less close than we might have anticipated, but the work has been revised without the discovery of any error. Relations such as:

$$r_{14} = r_{32}, \quad r_{16} = r_{52},$$

do not, however, appear to be theoretically necessary.

The problem now arises: are cross correlations between characters in husband and wife, solely due to selection of direct characters?

I think this may be roughly tested in the following manner. Suppose *only* these organs to be selected and the direct selection coefficients to be ρ_{12} , ρ_{34} , ρ_{56} , as before. They may be found from equations (i)* and we have the values:

$$\rho_{12} = \cdot 2374, \quad \rho_{34} = \cdot 0053, \quad \rho_{56} = \cdot 1043.$$

Thus there is most immediate selection of stature, a sensible selection of forearm, and practically none of span.

* These give numerically:

$$\cdot 2804 = \rho_{12} + \cdot 5919\rho_{34} + \cdot 3818\rho_{56},$$

$$\cdot 1989 = \cdot 5919\rho_{12} + \rho_{34} + \cdot 5087\rho_{56},$$

$$\cdot 1977 = \cdot 3818\rho_{12} + \cdot 5087\rho_{34} + \rho_{56}.$$

Now, if there be no *immediate* cross selection of other than these three organs and no immediate direct selection we should expect to find:

$$\left. \begin{aligned}
 r_{32} &= \rho_{12}r_{13} + \rho_{24}r_{24} + \rho_{56}r_{35}r_{26} \\
 r_{14} &= \rho_{12}r_{24} + \rho_{34}r_{13} + \rho_{56}r_{15}r_{46} \\
 r_{52} &= \rho_{12}r_{15} + \rho_{34}r_{35}r_{24} + \rho_{56}r_{26} \\
 r_{16} &= \rho_{12}r_{26} + \rho_{34}r_{31}r_{46} + \rho_{56}r_{15} \\
 r_{36} &= \rho_{12}r_{13}r_{26} + \rho_{24}r_{46} + \rho_{56}r_{25} \\
 r_{54} &= \rho_{12}r_{15}r_{24} + \rho_{34}r_{25} + \rho_{56}r_{46}
 \end{aligned} \right\} \dots\dots\dots (ii)$$

Substituting the ρ 's and the organic correlations in (ii) we find:

TABLE III.

Coefficients of Cross Assortative Mating.

Husband's Character	Wife's Character	Observed Value	Calculated Value
Span	Stature	·2023	·2327
Stature	Span	·1820	·2288
Forearm	Stature	·1784	·2171
Stature	Forearm	·1403	·2152
Span	Forearm	·1533	·1929
Forearm	Span	·1545	·1894

We conclude from this Table that: since the calculated values are all larger than the observed, the hypothesis that only direct selection of these three characters takes place is not valid. There must be direct selection of other correlated organs, or in some manner, as yet inexplicable, also an immediate cross assortative mating in man*. Generally, the results given in the present and the previous section for assortative mating, and in section (iv) for preferential mating, indicate that in future a greater degree of attention must be paid to sexual selection. It can hardly be so significant in the case of man, where most people would probably *à priori* suppose it of no account, and yet fail to play an important part in wild life. In particular, experimental enquiry on the relation of homogamy to fertility,—the likeness not being due to in-breeding—would be of very great value. It is clear, that “negative” † natural selection accompanied

* My own view, for which I have small evidence at present, is that the functions of sex are far more highly correlated with the physical characters in man than is generally supposed, and that the fertility of any given pair is very delicately atuned to the relative proportions of their frames. Hence when we come to correlate the physical characters in the parents of adult children, we find not only high direct but also high cross correlations, which seem inexplicable on any hypothesis of conscious assorting at mating. The only way to test this is to compare the correlations of husbands and wives at marriage with those of parents of adult children. We have already seen that these in certain cases sensibly differ. (See p. 373 and p. 374 footnote.)

† A selection for destruction not survival: see *Phil. Trans.* Vol. 200, A, p. 59.

by the correlation of homogamy and fertility would much aid us in comprehending the origin of species.

Although we are unable at present to account for the high coefficients of cross-assortative mating in man, it is possible to give an empirical formula, which will enable us to determine these coefficients in terms of the direct assortative mating coefficients and the organic correlations well within the limits of the probable errors of our results. Clearly the cross-assortative mating coefficients ought to vanish with both direct and organic correlations. Hence, if p, q refer to two organs in the husband and p', q' to the same pair in the wife, we should expect the cross correlation r_{pq} to be of the form :

$$r_{pq} = Cr_{pp'}r_{p'q} + C'r_{qq'}r_{pq}$$

Having satisfied myself that C and C' might be taken as practically equal, I found C as the mean of the last six entries in Table II. There resulted the formulae

$$\left. \begin{aligned} r_{pq} &= .5342 (r_{pp'}r_{p'q} + r_{qq'}r_{pq}), \\ r_{p'q} &= .5342 (r_{pp'}r_{pq} + r_{qq'}r_{p'q}), \end{aligned} \right\} \dots\dots\dots(iii)$$

whence I found the following results.

TABLE III bis.
Calculated and Observed Cross Coefficients in Husband and Wife.

Husband's Character	Wife's Character	Observed Value	Calculated Value	Difference
Span	Stature	.202	.198	+ .004
Stature	Span	.182	.196	- .014
Forearm	Stature	.178	.159	+ .019
Stature	Forearm	.140	.157	- .017
Span	Forearm	.153	.151	+ .002
Forearm	Span	.155	.151	+ .004

The differences are well within the probable errors, and the above formulae may I think be safely used, if the cross coefficients are unknown.

(vii) *Direct Parental Inheritance.*

For the resemblance in like organs between offspring and parents we have for our three organs twelve cases. The correlations deduced from Appendix Tables XXII.—XXXIII. are given in Table IV. below.

It is impossible to regard these results without extreme satisfaction, not only as confirmation of the general reliability of the material, but also for the weighty evidence they bring for the nature of inheritance in man. When one remembers the labour of collecting the measurements, the days spent in tabling and reducing it, and the doubts which not unnaturally arose as to its value and the value of the tedious labour spent on it, the sense of satisfaction felt may be considered pardonable. The surprising agreement of the results—well within the probable

errors—for each character is to be noted in the first place. Considering that the measurements are made on more than 4000 individuals of different sexes in more than 1000 families, the conviction is complete that these numbers correspond to a

TABLE IV.

Coefficients of Heredity. Parents and Offspring.

Character	Father and		Mother and	
	Son	Daughter	Son	Daughter
Stature	$\cdot 514 \pm \cdot 015$	$\cdot 510 \pm \cdot 013$	$\cdot 494 \pm \cdot 016$	$\cdot 507 \pm \cdot 014$
Span	$\cdot 454 \pm \cdot 016$	$\cdot 454 \pm \cdot 014$	$\cdot 457 \pm \cdot 016$	$\cdot 452 \pm \cdot 015$
Forearm	$\cdot 421 \pm \cdot 017$	$\cdot 422 \pm \cdot 015$	$\cdot 406 \pm \cdot 017$	$\cdot 421 \pm \cdot 015$

reality in nature. From them we may safely draw the following conclusions for the organs examined:

(a) The son and daughter are equally influenced by their father, and equally influenced by their mother.

While a change of sex does appear to weaken hereditary influence in the eye-colour of man*, it does not appear to have any perceptible influence on the size of the human frame.

(b) In their influence on offspring there is no average prepotency of either father or mother, whatever there may be in individual cases.

(c) The inheritance of all characters does not appear to be the same.

The inheritance of forearm is for all four cases sensibly less than the inheritance of span, and that of span less than that of stature. We might as a probability put forward the following statement for further investigation.

(d) The more complex a character the greater the intensity of hereditary resemblance.

The fact that the correlation falls below $\cdot 5$ with the simplicity of the character under consideration seems to suggest, however, that the reduction of the intensity cannot be due to an "alternative inheritance" in the case of the simple components of the character†.

For the mean values we have the following results:

Mean parental inheritance,	father to son:	$\cdot 463$
"	"	"
"	"	"
"	mother to son:	$\cdot 452$
"	"	"
"	"	"
"	to daughter:	$\cdot 460$
Mean parental inheritance for both sexes and all characters:		$\cdot 460$.

* *Biometrika*, Vol. II. pp. 237—240.

† See *R. S. Proc.* Vol. 86, p. 142, and *Natural Inheritance*, p. 139.

I think we may fairly take the intensity of inheritance for measurable characters in man to be .46, or even for rougher work .5. It may be as well to put on record here the principal results for heredity in the direct line so far reached. I omit the results obtained in my memoir of 1895*, for I consider my present data to replace that series.

TABLE V.
Parental Inheritance in Different Species.

Species	Character	Mean Value	No. of Pairs used	Source	Remarks
Man	Stature	.506	4886	Present Memoir	—
"	Span	.459	4873	ditto	—
"	Forearm	.418	4866	ditto	—
"	Eye Colour	.495	4000	<i>Phil. Trans.</i> Vol. 195, p. 106	—
Horse	Coat Colour	.522	4350	<i>Phil. Trans.</i> Vol. 195, p. 93	—
Basset Hound ...	Coat Colour	.524	823	<i>R. S. Proc.</i> Vol. 66, p. 154	Dams only used
Greyhound ...	Coat Colour	.507	9279	Unpublished data for two characters	Dams and Sires both used
Aphis (<i>Hyalopterus</i> } <i>Trirhodus</i>) ... }	Right Antenna Frontal Breadth	.439	366	<i>Biometrika</i> , Vol. I. p. 129	} Ratios only taken to free from growth factor
Daphnia Magna ...	Protopodite Body Length	.466	96	<i>R. S. Proc.</i> Vol. 65, p. 154.	

I consider that this table contains the most reliable data we yet have collected and reduced for parental influence on offspring.

The general mean of the whole of these series is .48 and so far as we have yet gone, we may I think conclude, that:

(a) There is no reason for supposing parental heredity to be stronger in one species than a second.

(b) Its values lie between .42 and .52 and cluster round .48.

Thus for most practical purposes we may assume parental heredity for all species and all characters to be approximately represented by a correlation of .5.

In the course of the past 8 years many cases of parental inheritance have been worked out by the biometricians associated with me at University College, some of the most important of these are still unpublished, others have been replaced by far more reliable data; in further cases we know that the material was doubtful, e.g. the cephalic index for *fathers* and children of the North American Indians, or *sire* and offspring in the Basset Hounds. In such cases better material has been sought and our first results modified †. But in the present controversial phase of

* *Phil. Trans.* Vol. 187, p. 253 *et seq.*

† For example the greyhounds have shown that anomalies of the Basset Hound results were peculiar to the material, the cephalic index is inherited quite normally when we test it on material with reliable parentage, etc. etc.

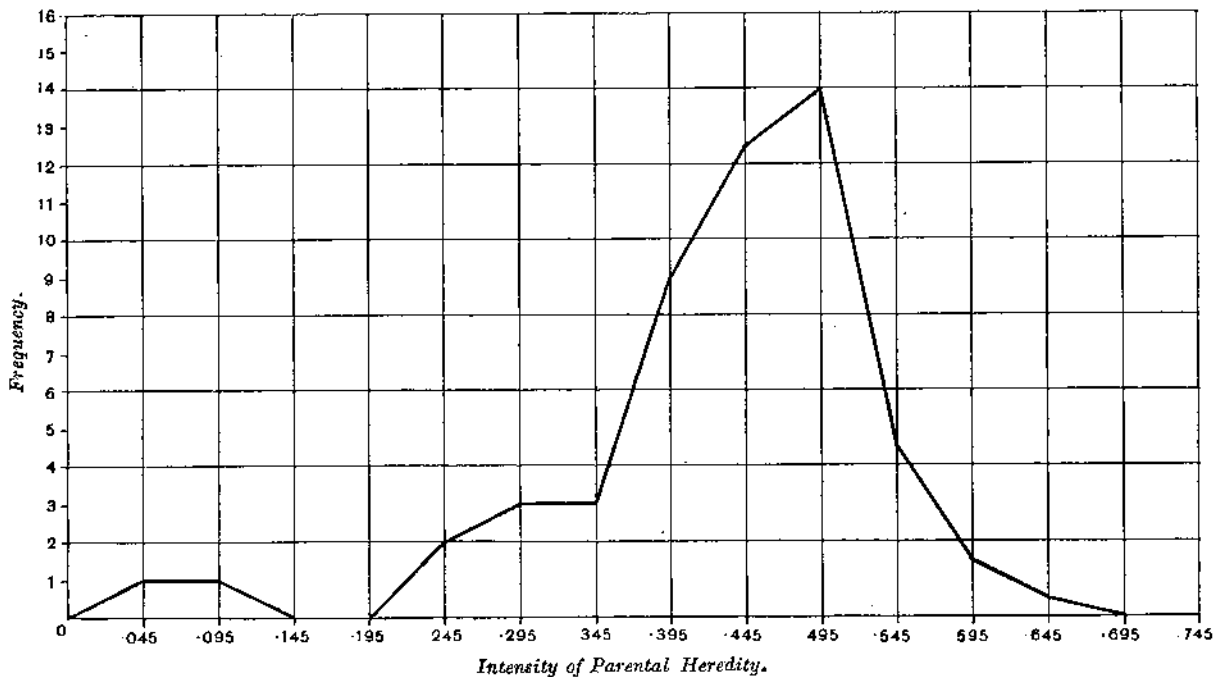
the theory of heredity, it seems well to hold no material back simply because one knows it to be untrustworthy. I therefore give the frequency distribution for every coefficient of parental correlation I am aware of, neither weighting them with the number of pairs on which they are based, nor remarking on the relative reliability of the data, which covers plants, insects and animals.

Frequency Distribution of Correlation Coefficients of Parental Heredity.

Magnitude of Correlation	.02-.07	.07-.12	.12-.17	.17-.22	.22-.27	.27-.32	.32-.37	.37-.42	.42-.47	.47-.52	.52-.57	.57-.62	.62-.67	Total
Frequency	1	1	—	—	2	3	3	9	12.5	14	4.5	1.5	.5	52

This distribution is represented graphically in the accompanying diagram; the mean and standard deviation of the system are $.430 \pm .010$ and $.107$ respectively. The fact of the cluster and its quantitative intensity are thus rendered obvious. The four extreme observations on the left are due to the Basset Hound Sires and North American Indian Fathers, both involving doubtful paternity*. If we omit

DIAGRAM VII. *Distribution of Correlation Coefficients in 52 Cases of Parental Heredity.*



* Both series are also very small, 100 to 400, as compared with the 1000 or more of most of the other series. As to their questionable character see *R. S. Proc.* Vol. 62, p. 414, and Vol. 66, p. 158 and especially footnote p. 159.

these as most certainly questionable the mean result is $\cdot453 \pm \cdot007$, the standard deviation being $\cdot071$. Thus $\cdot45$ may, I think, be justifiably taken in future to represent the approximate value of parental heredity, in cases where no direct observations have been made for the character and species under consideration. I prefer, however, the $\cdot46$ to $\cdot5$ of the *best* of the above series.

I now pass to the prediction formulae, i.e. the regression lines and planes, from which the probable value of a character in the offspring may be determined when the value of the character in the parentage is known.

If the subscript *c* denote child and *p* parent; and *m* be the mean, *C* the character; we have for prediction from one parent :

$$C_c = m_c + \frac{r_{cp}\sigma_c}{\sigma_p} (C_p - m_p) \dots\dots\dots (iv)$$

with a standard deviation for the array of value $\Sigma_c = \sigma_c \sqrt{1 - r_{cp}^2}$.

If we predict from two parents *p*₁ and *p*₂, the formula is :

$$C_c = m_c + \frac{r_{cp_1} - r_{cp_2}r_{p_1p_2}}{1 - r_{p_1p_2}^2} \frac{\sigma_c}{\sigma_{p_1}} (C_{p_1} - m_{p_1}) + \frac{r_{cp_2} - r_{cp_1}r_{p_1p_2}}{1 - r_{p_1p_2}^2} \frac{\sigma_c}{\sigma_{p_2}} (C_{p_2} - m_{p_2}) \dots (v)$$

with a standard deviation for the array of

$$\Sigma_c = \sigma_c \sqrt{\frac{1 - r_{cp_1}^2 - r_{cp_2}^2 - r_{p_1p_2}^2 + 2r_{cp_1}r_{cp_2}r_{p_1p_2}}{1 - r_{p_1p_2}^2}}$$

Using these formulae we have the following results* :

A. *Stature.*

For Son :

- (1) Probable Stature = $33''\cdot73 + \cdot516$ (Father's Stature) $\pm 1''\cdot56$,
- (2) Probable Stature = $33''\cdot65 + \cdot560$ (Mother's Stature)† $\pm 1''\cdot59$,
- (3) Probable Stature = $14''\cdot08 + \cdot409$ (Father's Stature)
 $+ \cdot430$ (Mother's Stature) $\pm 1''\cdot42$.

For Daughter :

- (4) Probable Stature = $30''\cdot50 + \cdot493$ (Father's Stature) $\pm 1''\cdot51$,
- (5) Probable Stature = $29''\cdot28 + \cdot554$ (Mother's Stature) $\pm 1''\cdot52$,
- (6) Probable Stature = $10''\cdot82 + \cdot386$ (Father's Stature)
 $+ \cdot431$ (Mother's Stature) $\pm 1''\cdot33$.

* The actual tables of correlation are given in the Appendix and from them it will be seen that all possible pairs were used in each case for determining the correlation. Thus the standard deviations and means vary slightly from table to table, of course well within their probable errors. The formulae here given were, however, obtained by using the means and standard deviations which were adopted for Table I.

† If Father and Mother are to contribute indifferently to Son's stature, the parental statures should be in the ratio of about 560 to 516, which is very nearly the ratio of 1·085 to 1, and almost exactly equal to the 1·083 to 1 of ratio of Father's to Mother's average stature.

B. *Span.**For Son:*

- (7) Probable Span = $38''\cdot46 + \cdot458$ (Father's Span) $\pm 1''\cdot89$,
 (8) Probable Span = $38''\cdot38 + \cdot511$ (Mother's Span) $\pm 1''\cdot88$,
 (9) Probable Span = $18''\cdot04 + \cdot375$ (Father's Span)
 $+ \cdot423$ (Mother's Span) $\pm 1''\cdot70$.

For Daughter:

- (10) Probable Span = $34''\cdot20 + \cdot425$ (Father's Span) $\pm 1''\cdot77$,
 (11) Probable Span = $34''\cdot18 + \cdot473$ (Mother's Span) $\pm 1''\cdot77$,
 (12) Probable Span = $14''\cdot70 + \cdot355$ (Father's Span)
 $+ \cdot394$ (Mother's Span) $\pm 1''\cdot61$.

C. *Forearm.**For Son:*

- (13) Probable Forearm = $10''\cdot65 + \cdot430$ (Father's Forearm) $\pm ''\cdot60$,
 (14) Probable Forearm = $10''\cdot88 + \cdot463$ (Mother's Forearm) $\pm ''\cdot60$,
 (15) Probable Forearm = $5''\cdot58 + \cdot362$ (Father's Forearm)
 $+ \cdot383$ (Mother's Forearm) $\pm ''\cdot56$.

For Daughter:

- (16) Probable Forearm = $9''\cdot43 + \cdot400$ (Father's Forearm) $\pm ''\cdot56$,
 (17) Probable Forearm = $9''\cdot40 + \cdot445$ (Mother's Forearm) $\pm ''\cdot56$,
 (18) Probable Forearm = $4''\cdot50 + \cdot334$ (Father's Forearm)
 $+ \cdot371$ (Mother's Forearm) $\pm ''\cdot51$.

On the right is given in each case the probable error of the prediction*. We see from these formulae that with the selection of one parent only, the offspring rise to within 40 to 50 per cent. of the selected value; with the selection of *both* parents to within 70 to 80 per cent. of it. The diminution of the variability of the array due to two selected parents, is however only slightly less than that due to the selection of one parent only.

If we selected for two generations we should have offspring the same very nearly as the selected ancestry†. With our values for parental correlation, it is obvious that two or three generations of selection will suffice to bring the average of the offspring sensibly up to the selected ancestry, and the regression after this,

* In using these formulae for prediction, those not fully conversant with statistical theory, must bear in mind that they give only the mean or most probable results of a whole array of offspring due to *all* parents of definite characters. The validity of the formulae cannot be tested on merely individual cases. This warning is necessary because I have so often had *individual* cases in man or dogs cited as upsetting the whole of the ancestral law!

† "The Law of Ancestral Heredity," *Biometrika*, Vol. II, pp. 221—6.

if the stock mates with its like, will be very small or zero*. We cannot unfortunately on the present material determine absolutely its value; for, in the first place we have no correlations with grandparents or higher ascendants, and in the second place the assortative mating coefficients are so large, that we cannot afford to neglect them to a first approximation, as we have done for the case of eye-colour in man and coat-colour in horses†.

What, however, the present investigation impresses upon one is this: Parental correlation being from .45 to .5 in value is much higher than we could anticipate from Mr Galton's *Natural Inheritance* data. Hence selection is far more rapid in its effects than we supposed a few years ago, two to four generations suffice to effect what we originally considered would need 6 to 8. Further, the regression after such selection may well be zero. I have not worked out yet the multiple regression formulæ allowing for assortative mating; they present considerable difficulty owing to the complexity introduced by the correlations between relations-in-law due to such mating. But neglecting for a moment the effect of assortative mating, the series of ancestral correlations,

$$\cdot 46 \quad \cdot 32 \quad \cdot 23 \quad \cdot 16$$

proceeding by a factor .7 would give a zero-regression and not differ widely from the ancestral correlations we know for eye-colour in man‡. I lay no stress on these particular numbers, but I wish to emphasise the point that a few generations of selection in the case of man suffice to establish a breed, and that regression for this breed may well be insensible.

(viii) *Cross Parental Inheritance.*

I have defined *cross* heredity to be the correlation of two different organs in two blood relations§. We are now for the first time in a position to estimate its magnitude.

We see at once that these coefficients of cross heredity are for some cases almost as large as the coefficients of direct heredity, and on the whole sensibly larger than the values which but a few years ago were supposed to be those of the

* The physical aspect of this is perfectly easy to understand. When we select one parent the offspring advance 35 to 40 p.c. on the general population, when we select two parents 70 to 80 p.c. If we select two parents and four grandparents, there is another percentage increase which brings us up into the 90 per cents., and if we select for three generations we have nearly the 100 per cent. of the required character. Now suppose the selected stock to inbreed or otherwise mate with its likes for this special character. Why will the regression now that selection ceases be zero or insensible? For this simple reason, that while we cease to select within the stock, yet each new generation has an additional selected generation of ancestry behind it, and the influence of this ancestry balances the regressional tendency. This is the simple verbal explanation of the cessation of regression with selection. The algebraical expression of its possibility was first given in my memoir of 1898: see *R. S. Proc.* Vol. 62, p. 401.

† *Ibid.* p. 224. See also *R. S. Proc.* Vol. 62, p. 388.

‡ *Biometrika*, Vol. II. p. 222. ϵ and ρ of p. 224 would be .56 and .44 respectively.

§ *Phil. Trans.* Vol. 187, A, p. 259. See also *R. S. Proc.* Vol. 62, p. 410.

direct coefficients. We have thus, if it were needed, still further evidence that the original estimates of the strength of heredity were far too low.

TABLE VI.

Cross Parental Heredity Coefficients.

Parent	Parent's Character	Offspring	Offspring's Character	Correlation and Probable Error
Father ...	Stature	Son	Span	$\cdot418 \pm \cdot017$
" ...	Span	"	Stature	$\cdot399 \pm \cdot017$
" ...	Stature	"	Forearm	$\cdot370 \pm \cdot018$
" ...	Forearm	"	Stature	$\cdot355 \pm \cdot018$
" ...	Span	"	Forearm	$\cdot399 \pm \cdot017$
" ...	Forearm	"	Span	$\cdot400 \pm \cdot017$
Father ...	Stature	Daughter	Span	$\cdot423 \pm \cdot015$
" ...	Span	"	Stature	$\cdot407 \pm \cdot015$
" ...	Stature	"	Forearm	$\cdot341 \pm \cdot016$
" ...	Forearm	"	Stature	$\cdot383 \pm \cdot016$
" ...	Span	"	Forearm	$\cdot382 \pm \cdot016$
" ...	Forearm	"	Span	$\cdot396 \pm \cdot015$
Mother ...	Stature	Son	Span	$\cdot424 \pm \cdot017$
" ...	Span	"	Stature	$\cdot390 \pm \cdot017$
" ...	Stature	"	Forearm	$\cdot356 \pm \cdot018$
" ...	Forearm	"	Stature	$\cdot344 \pm \cdot018$
" ...	Span	"	Forearm	$\cdot345 \pm \cdot018$
" ...	Forearm	"	Span	$\cdot365 \pm \cdot018$
Mother ...	Stature	Daughter	Span	$\cdot431 \pm \cdot015$
" ...	Span	"	Stature	$\cdot385 \pm \cdot016$
" ...	Stature	"	Forearm	$\cdot387 \pm \cdot015$
" ...	Forearm	"	Stature	$\cdot318 \pm \cdot016$
" ...	Span	"	Forearm	$\cdot370 \pm \cdot016$
" ...	Forearm	"	Span	$\cdot362 \pm \cdot016$

One of the most difficult points to be sure about is the theoretical relationship which is to be expected between the intensities of direct and cross inheritance. If (i) all organs and characters were inherited at the same rate, and (ii) the organic correlations in younger and older generations were the same, and (iii) the variabilities of these generations, as measured by their coefficients of variability, were the same, then it follows that the mean of two corresponding coefficients of cross heredity is the product of the coefficient of direct heredity into the organic correlation*. But none of the three conditions stated above is accurately fulfilled, as we have seen, in the present material. Notably we find sensible divergence from the first. We may possibly attempt to allow for the first disturbing factor in the following manner: the cross-correlations should vanish (a) when the direct

* *R. S. Proc.* Vol. 62, p. 411.

heredity is zero, and again (b) when the organic correlations are zero. Hence we might, if 1, 2 represent organs in one of a pair, and 1', 2' the same organs in the other of a pair of relatives, expect to find :

$$r_{12} = c r_{11'} r_{1'2'} + c' r_{22'} r_{12}$$

$$r_{1'2'} = c'' r_{22'} r_{1'2'} + c''' r_{11'} r_{12}$$

where c, c', c'' and c''' are at present indeterminate.

Hence :

$$\frac{1}{2} (r_{12} + r_{1'2'}) = r_{1'2'} \left(\frac{c r_{11'} + c'' r_{22'}}{2} \right) + r_{12} \left(\frac{c' r_{22'} + c''' r_{11'}}{2} \right).$$

Now if heredity were constant for all characters, we should have $r_{11'} = r_{22'}$, and we should reach the above proposition by putting $c = c' = c'' = c''' = .5$. Thus we should expect the c 's to be equal to .5 plus functions of $r_{11'}$, $r_{22'}$, r_{12} and $r_{1'2'}$, which vanish when $r_{11'} = r_{22'}$ and $r_{12} = r_{1'2'}$. What those functions may be it would probably be hard to determine. I therefore propose to write simply

$$\begin{aligned} r_{12} &= C (r_{11'} r_{1'2'} + r_{22'} r_{12}) \\ r_{1'2'} &= C (r_{22'} r_{1'2'} + r_{11'} r_{12}) \end{aligned} \dots\dots\dots (vi)$$

and determine the values of C . These are given in the Table VII. below. We see at once that C is always greater than .5, its mean value is .5683. If we adopt this value we should have the following empirical formula to determine a cross heredity coefficient :

$$r_{12} = .5683 (r_{11'} r_{1'2'} + r_{22'} r_{12}) \dots\dots\dots (vii).$$

But since the numerical factor is greater than .5, and $r_{11'}$ and $r_{22'}$ as a rule somewhat less, we ought to get rough values of the cross coefficients from

$$r_{12} = \frac{1}{4} (r_{1'2'} + r_{12}) \dots\dots\dots (viii).$$

The values calculated from these empirical formulae are given in Table VIII. below with the differences.

The probable errors of these coefficients of cross correlations are given in Table VI. Formula (vii) gives 13 values above and 11 below the corresponding probable error. Formula (viii) gives 11 above it and 13 below it. The mean deviation of (vii) is .019 and (viii) is also .019. Thus the formulae are practically equally good so far. But (vii) gives 10 above and 14 below, while (viii) gives only 3 above and 21 below the observed values. Thus as an empirical formula (vii) is somewhat better than (viii), which is really based on the equality of all inheritance coefficients and their approximation to a value of .5, assumptions only roughly true.

Practically either (vii) or (viii) would suffice for most purposes, and the manner in which they smooth the observed results, especially in making what we might *a priori* expect, near equality* between the pairs of corresponding cross correlations is itself an argument in their favour. Hence I should say that when the

* See *R. S. Proc.* Vol. 62, p. 411.

organic correlations and direct heredity coefficients are known the cross heredity coefficients may be found very closely from formula (vii). If the organic correlations are known, but no heredity coefficients at all, then the direct heredity coefficients may approximately be taken as equal to .5 and the cross heredity coefficients approximately found from the organic correlations by formula (viii).

(ix) *Direct Fraternal Resemblance.*

I now turn to the observed degree of resemblance between brothers and sisters for the three characters we have measured in our Family Records. We have the following results:

TABLE IX.
Correlation Coefficients for Direct Fraternal Heredity.

Character	Brother and Brother	Sister and Sister	Brother and Sister	Mean
Stature	.511 ± .028	.537 ± .022	.553 ± .013	.534
Span	.549 ± .026	.555 ± .021	.525 ± .013	.543
Forearm	.491 ± .029	.507 ± .023	.440 ± .015	.479
Mean	.517	.533	.506	.519
Eye Colour*	.517 ± .020	.446 ± .023	.462 ± .022	.475
Total mean	.517	.511	.495	.508

Now there are certain differences in the entries in this Table, thus resemblance in siblings seems greater for stature and span, than for forearm or eye-colour, and again the resemblance of brother and sister seems on the average slightly smaller than the resemblance between siblings of the same sex. There are also certain irregularities, which I have no means of accounting for, and which seem larger than can be explained by random sampling†. Still there cannot be the least doubt from the above table that .5 measures very closely the average degree of hereditary resemblance in human siblings, and that the correlation clusters closely round this value. As in the case of parental heredity we see a most marked increase in the intensity of hereditary resemblance when we compare our results with those obtained for stature some years ago‡. If we compare our Family Records with the School Records, of which I only cite at present the results for brothers, we

* Francis Galton's eye-colour record reduced for my paper on Heredity in Man in *Phil. Trans.* Vol. 195, A, p. 106.

† The material, as the reader will see by consulting the actual tables, is far less.

‡ *Phil. Trans.* Vol. 187, A, p. 281. It was the difficulties associated with the data used in 1895 (see especially pp. 283—5 of above memoir) that led to the collection of heredity data which has been in progress since 1894.

find good agreement in the .5 value. In the Table below each series involves 1000 to 2000 cases.

TABLE X.
Fraternal Resemblance in Boys at School.

Character	Correlation	Character	Correlation
General Health... ..	.520	Cephalic Index	.486
Eye Colour539	Head Length	.504
Hair Colour621	Head Breadth	.593
Straightness of Hair498	Auricular Height	.554

Mean of Eight Characters .539.

This compares well with .517 of the above Family Records for Brothers. At the same time several of the above results are under revision, namely the absolute measurements of the head. In this case every boy was reduced to a standard age 12 by adding to or subtracting from his age the *average* growth found to take place between his age at measurement and the age of 12. A more subtle method of determining the allowance to be made for growth has been recently given by me in a paper published this year, only it involves a very great amount of numerical work, i.e. five instead of two correlation tables, and thus we have only been able so far to modify the correlation in the matter of head length*. I consider it better, however, to place above the correlations as found by one uniform method until we are in position to publish all the results revised. I anticipate that both head breadth and auricular height will ultimately be found to be really nearer to .5 than appears above. Meanwhile it seems quite safe to sum up our results for fraternal correlation in man as follows:

- (i) The degree of resemblance of brethren is closely the same for all characters.
- (ii) The two sexes appear to be equally influenced by heredity.
- (iii) The intensity of fraternal correlation in man is close to .5, possibly slightly greater. But for practical purposes we may conveniently work with $\frac{1}{2}$ as a round number.

I now turn to what personally I consider one of the most obscure points in the quantitative determination of inheritance, namely: the manner in which fraternal resemblance varies from species to species, while paternal inheritance remains fairly constant. If we look at Table V. we see that within moderate limits parental influence approximates to the same value for very different species and very diverse characters. This cannot be asserted with the same accuracy of fraternal correlation. I have found values of it ranging from .4 to .7 for large and

* *R. S. Proc.* Vol. 71, pp. 290—4.

apparently very trustworthy data for different species. I attribute this, although I have not been able at present to verify it, to *prepotency**. In dealing with prepotency I think it important to distinguish *ab initio* between three kinds: *sex-prepotency*, *unit prepotency*, and *intermittent prepotency*. By *sex-prepotency* I understand that the offspring of one or other sex or of both sexes are more like the male or the female parent as the case may be. Its existence is demonstrated by showing that the correlation for one parent with all the offspring or with one class of offspring is greater than for the other parent. An examination of Table IV. seems to prove that in man for stature, span and forearm there exists no sex-prepotency. On the other hand in eye-colour in man, there does appear to be a *differential sex-prepotency*, fathers are prepotent over mothers for eye-colour in sons, and mothers are prepotent over fathers for the same character in daughters*. If the paternal record were trustworthy in the case of Basset Hounds—which I am very doubtful about—then there would be a large sex-prepotency for all offspring of the dam over sire in coat-colour†. From this sex-prepotency must be distinguished an individual prepotency which I term *unit prepotency*, and which is independent of sex. In unit prepotency one or other unit in a mating is prepotent owing to the possession of some physical character, other than a sexual character. This physical character may or may not be that in which the prepotency shows itself in the offspring. Thus it is conceivable that a dark-eyed parent of either sex might have a unit prepotency over a light-eyed parent, not necessarily in eye-colour or in eye-colour only, but possibly in hair-colour, or stature or mental characters. The unit prepotency may, however, in no way depend upon a simple observable character like this, but on a subtle combination of physical factors producing individual prepotency in one unit of the pair. To demonstrate the latter form of unit prepotency will always be a difficult problem; it could possibly be attacked by considering the reduction of variability in the array of offspring of supposed unit prepotent matings below the average variability of arrays in which such prepotency is supposed not to exist. This method would hardly be possible in the case of man where the number of offspring is too small to get the variability of an array free from a very large probable error. It might be effective in the case of snails, moths, many insects and plants with numerous offspring. When unit prepotency is supposed to be associated with the possession of a definite physical character, it is perfectly possible to attack the problem by the method of association, i.e., investigating the association between the presence (or absence) of this character in a parent and the ratio to total offspring of offspring in the array who do (or do not) possess this character, or some other character of the parent in question. If unit prepotency were absolute we should have the case of "dominance" as originally propounded by Mendel.

While we suppose unit prepotency,—the tendency of one individual out of a pair to be prepotent,—to be *chronic*, there is another form of prepotency which we may describe as *intermittent*. One or other parent may at a particular mating, or

* *Phil. Trans.* Vol. 195, A, p. 106. See also F. Lutz, *Biometrika*, Vol. II. p. 234.

† *R. S. Proc.* Vol. 66, p. 157.

may in certain individual offspring of one and the same mating, be prepotent. On another occasion, or in other offspring of one and the same mating, it may not be prepotent or even the other parent may be prepotent. Such prepotency might exhibit itself in "alternative" or "exclusive" inheritance*, and is distinct from any unit prepotency or absolute or partial dominance. It does not depend on the possession by one mate of certain characters, but on the condition of the parents and other circumstances peculiar to a special mating.

Now the fundamental point to be borne in mind is this, that apart from sex-prepotency, neither unit prepotency nor intermittent prepotency need in any way influence the parental correlations. The average resemblances of offspring to either parent will not be affected if in some matings the mother, in other the father is prepotent. Nor again will it be affected, if occasionally the two parents are intermittently prepotent. But such types of prepotency will largely influence the degree of resemblance between brethren. If, either invariably or intermittently, one parent is prepotent, the offspring of all matings of these parents or the offspring of one litter will be more alike, than the offspring of another species in which such prepotency does not exist. When therefore we find parental correlation the same for a number of species and fraternal correlation different, I am strongly of opinion that this will be found to be due to differing amounts of unit prepotency or of intermittent prepotency or of both combined in diverse species. I have already insisted on this effect of prepotency in disturbing fraternal correlation†, but it seemed necessary again to refer to it as the probable explanation of the great differences observable in the fraternal correlations given below in Table XI.

TABLE XI. Fraternal Correlation in Different Species.

Species	Characters	Brother and Brother	Sister and Sister	Sister and Brother	All Siblings
Man	Family Records. Mean of } three characters ... }	.517	.533	.506	.519
"	Eye Colour517	.446	.462	.475
"	School Records. Mean of } sixteen characters ... }	.520	.519	.518	.519
Basset Hound ...	Coat Colour for same litter	—	—	—	.508
Greyhound ‡ ...	Amount of Red in Coat, } same litter ... }	.683	.710	.707	.700
"	Amount of Black in Coat, } same litter ... }	.642	.680	.659	.660
Thoroughbred Horse	Coat Colour623	.693	.583	.633
Daphnia (<i>Magna</i>) ...	Ratio of Protopodite to } Body Length ... }	—	—	—	.693
Aphis (<i>Hyalopterus</i> } <i>Trirhodus</i>) ... }	Ratio of Right Antenna to } Frontal Breadth ... }	—	—	—	.589

* *R. S. Proc.* Vol. 66, p. 141, etc. and *Phil. Trans.* Vol. 195, A, p. 89 *et seq.*† *R. S. Proc.* Vol. 66, p. 152, and *Phil. Trans.* Vol. 195, A, p. 101.

‡ Unpublished results, tabled by Miss A. Barrington from Mr Howard Collins' data, reduced by Dr A. Lee.

I have not placed in this table the results for stature as found from Mr Galton's Family Data, nor those for Cephalic Index for North American Indians, because I consider that the results for both these characters are replaced by the larger series we have now at our disposal, and which are included under "man" in the above list. Otherwise it embraces nearly all the data we have as yet at our disposal. Now it is clear that the value for man is about .5 and agrees well with the value found for Basset Hounds, and indeed with that for the Shirley Poppy, assuming complete cross fertilisation*. On the other hand the horses and greyhounds, *while agreeing well with man for the parental correlations* (see Table V. p. 23), show a much increased fraternal correlation of the same order as that between the parthenogenetic offspring of *Daphnia* and *Aphis*†. Now how far is this due to such factors as unit prepotency or intermittent prepotency? All we can do at present is to suspend our judgment on this point. In the case of dogs, intermittent prepotency might manifest itself by the offspring of the same parents for the same litter being more alike than for different litters. Now will this account for the high values of the greyhound results? Unfortunately our records contain only greyhounds of the *same* litter, all members being recorded, while the volumes of the greyhound stud-book contain only a *selection* of all dogs born, colour undoubtedly being a selected character. Further it is very difficult from those volumes to extract a sufficient number of brethren of full blood from different litters. Still we hope to be able to throw some light on the problem of at least intermittent prepotency in the case of greyhounds. It is remarkable that the fraternal correlation in the Basset Hounds, while according closely with that in man, is the same sensibly in intensity for siblings from the same and from different litters. The case of the thoroughbred horses is somewhat different, but here we propose to draw up separate tables for twin foals and foals from the same parents in different years, and thus if possible differentiate intermittent prepotency, if it really exists. The high values, however, found for half-siblings in the case of the thoroughbreds seem to indicate that we must look rather to unit prepotency than intermittent prepotency for the source of the high value of fraternal as compared with parental correlation in the case of the horse.

What is quite clear is that we badly want the *measurement* of further characters for siblings in both mammals and insects. The present results show that while the value .5 has overwhelming evidence for it in the case of both measurable and unmeasurable characters in man, we are yet without like data for the measurable characters in horse, dog or any other mammal. Should these ultimately be found to agree with the results given above for the quantitatively unmeasurable characters, I personally hold at present, that the solution for equal parental and unequal fraternal correlations in these different species should first be sought in a fuller study of unit and intermittent prepotency.

* *Biometrika*, Vol. II. p. 81.

† In the case of these insects differential environment may, of course, have emphasised the resemblance.

(x) *Cross Fraternal Resemblance.*

I turn to the relationships between different organs in pairs of siblings. These are tabulated below.

TABLE XII.

Correlation Coefficients for Cross Fraternal Heredity.

1st Sibling	Character	2nd Sibling	Character	Correlation and Probable Error
Brother	Stature	Brother	Span	.444 ± .021
"	Stature	"	Forearm	.368 ± .023
"	Span	"	Forearm	.451 ± .021
Sister	Stature	Sister	Span	.471 ± .017
"	Stature	"	Forearm	.438 ± .018
"	Span	"	Forearm	.453 ± .017
Brother	Stature	Sister	Span	.478 ± .014
"	Span	"	Stature	.456 ± .014
"	Stature	"	Forearm	.399 ± .015
"	Forearm	"	Stature	.412 ± .015
"	Span	"	Forearm	.419 ± .015
"	Forearm	"	Span	.423 ± .015

The same general remark must again be made here, i.e. these cross-correlations are remarkably high,—as high as a few years ago we anticipated that the direct fraternal correlations would be.

The series being rather short—three to four hundred brothers*—the results are more irregular than we might have hoped for. In particular the cross-correlation between brother's stature and brother's forearm is distinctly less than we might have expected. A result of slightly over .4 would clearly be more consonant with the other results, but I have not been able to discover any slip in the arithmetic. In the brother-sister correlations we find that within the limits of the probable errors of random sampling the cross-correlation coefficients are pair and pair equal, e.g. the relation of brother's stature to sister's forearm is sensibly that of brother's forearm to sister's stature.

To obtain an empirical formula, I assumed that as in (vi) p. 385 we should have

$$r_{12} = C(r_{11}r_{12} + r_{22}r_{12}) \dots\dots\dots (ix).$$

I determined C from the twelve series and found for its mean value .5585. This is within two per cent. of the value of C found for the cross-parental relationships, and I think the agreement is as close as we could hope for†.

* See Appendix of correlation tables.

† To obtain the desirable end of using one formula instead of two. I am not convinced that equality is *à priori* to be expected.

Using the formula

$$r_{12} = .5585 (r_{11}r_{22} + r_{21}r_{12}) \dots\dots\dots (x),$$

I find the following results given in Table XIII. The agreement of the observed and calculated results is not as close as in the previous case of cross-parental heredity, but the series from which the observed values are determined are not half as large. Further, the calculated values depend on the coefficients of direct collateral inheritance, and in working out these we have always correlated elder with younger brother. On the other hand it did not seem worth while in calculating the cross-coefficients to separate our rather small amount of material up into two groups and distinguish between the relationship of, say, stature of elder brother to span of younger brother, and again, stature of younger brother to span of elder brother. This difference of treatment is no doubt a source of some of the observed irregularity, but the bulk of it is due to the smallness of our group of brothers.

The mean error of the results from (vii) is .019 and from (x) is .020, but (vii) has errors of .043, .043 and .039 larger than the maximum .034 reached by (x). The first formula gives seven values greater and five less, the second formula gives six greater and six less than the corresponding probable errors in Table XII. Thus on the whole Formula (x) is slightly the better, but the advantage is so small that for practical convenience (vii) might be well used for both. I do not see why the numerical factors in (x) and (vii) should necessarily be equal or nearly equal; still less is there any reason why the factors in these blood relationship formulae should be nearly equal to the value of the factor in (iii), the empirical formula for assortative mating. But it is worth noting that for most practical purposes a common formula with a mean numerical factor of .555 will give results quite within the limits of the probable errors of our material.

It thus appears that my original proposition as to cross-heredity, based on the assumptions of equality of all inheritance-coefficients and of the corresponding organic correlations in the pair of relatives, is not correct; the factor of .5 in the original proposition has in the case of man to be replaced by a value lying between .5 and .6, the mean value being .555. We have not at present material enough to test how far this number has any validity beyond cross-heredity in man*. The cases I have data for, however, do show an excess over .5 of the same order as we find in the case of man, and I hope shortly to publish further results for cross-heredity, closely bearing on this point.

(xi) *General Conclusions.*

If readers of the present paper feel that on certain points it is inconclusive, I think this must be largely attributed to the inherent difficulties of the subject. The further we advance, the more complex the problem becomes, and the wider

* A short series in *Aphis* has been dealt with by Dr Warren: see *Biometrika*, Vol. 1. p. 142. The value of the factor there given is .5 for one character and .68 for the second, giving a mean parental factor of .59 for *Aphis* as against .56 for man.

TABLE XIII.
Observed and Calculated Values of Cross Fraternal Coefficients.

Pair of Characters	Brother and Brother			Sister and Sister			First Brother and Second Sister					
	From (vii)		From (x)	From (vii)		From (x)	From (vii)		From (x)			
	Calculated	Δ	Calculated	Δ	Calculated	Δ	Calculated	Δ				
Stature and Span483	-.039	.475	-.031	.514	-.043	.505	-.034	.499	-.021	.491	-.013
Span and Stature ...	—	—	—	—	—	—	—	—	.499	-.043	.490	-.034
Stature and Forearm391	-.023	.384	-.016	.425	+.013	.417	+.021	.397	+.002	.390	+.007
Forearm and Stature ...	—	—	—	—	—	—	—	—	.395	+.017	.388	+.024
Span and Forearm448	+.003	.440	+.011	.432	+.021	.425	+.028	.420	-.001	.412	+.007
Forearm and Span ...	—	—	—	—	—	—	—	—	.419	+.004	.412	+.011

Δ = Observed - Calculated Value.

the range of new problems which suggest themselves for solution. Yet I think each large mass of material statistically reduced places a further stratum of firm ground beneath us. In particular, this first paper on inheritance of the physical characters in man, has, I hold, enabled us to reach some very definite results. Indeed, I believe them sufficient repayment for the years spent by my helpers in measuring upwards of a thousand families and tabling and reducing the data*. Of the special results obtained I would refer in particular to the following.

(i) We have very definite evidence that the normal curve suffices to describe within the limits of random sampling the distribution of the chief physical characters in man.

This confirms the conclusions of Galton, Macdonell, Fawcett and other workers in anthropometry, and is of special value when we come to extend our results to the inheritance of characters not quantitatively measurable.

(ii) The regression curve between pairs of blood relations, whether we deal with direct or cross-heredity, is within the limits of random sampling *linear*. This had been already suggested by Galton on the basis of the theory of normal distribution, and confirmed by his researches on stature. I think we may safely assume in future that the dimensions of the human body give linear regression-lines†.

(iii) There is an apparent change in type going on in man, especially evidenced in the female, but also sensible in the male. The young adult differs in magnitude, variability and correlation from the old adult and the difference appears to be significantly beyond growth changes.

We cannot at present determine whether this change is:

(a) Environmental, due to change in physical training and food between the young and old generations.

(b) Due to natural selection, the young adults being reduced nearer to the old adult type by deaths of a selective character in the intervening 20 to 30 years. If the change of type is due to a selective death rate, it may be either periodic, occurring in each generation, or secular, i.e., a progressive change.

(c) Due to reproductive selection, out of young adults a certain class have a differential fertility and become in bulk the parents of adult offspring.

But although we are not in a position to effectually discriminate at present between the amount of change due to (a), (b) and (c), our results immensely emphasise the view that even in apparently unessential characters mankind is, even at the present day, not in a stable condition, but that a change of type is very probably taking place owing to natural or reproductive selection or environmental

* When it is remembered that the whole work of measurement was done by volunteer aid, and without assistance from any public fund, I think other workers may take heart, who imagine that problems in heredity are necessarily confined to extensive breeding experiments of an expensive nature.

† This is really a very important point. In a forthcoming memoir on skew correlation, I deal with non-linear regression and show how fairly frequent it is and how complex it renders the treatment of correlation.

influence, and the change is of a magnitude, which would accumulate, if it be secular, within a comparatively few centuries into most significant differences.

(iv) There is a quite unexpected amount of sexual selection even of the physical characters in man. There is probably preferential mating, there is most certainly a large amount of assortative mating, and this not only in the same but in cross characters. The *modus operandi* of this assortative mating is not clear; it can hardly in any great part be due to conscious selection; it may be the result of reproductive selection, i.e. a subtle combination of physical characters in male and female being most likely to give a pair with a number of adult children. Be the source what it may, the existence of this assortative mating most substantially modifies the form of biparental inheritance, and its existence can hardly in future be neglected when we are considering the problems of heredity.

(v) The coefficient of parental heredity varies to some extent from character to character in man, having a mean value of about .46. This value is, however, in quite close agreement with the results obtained for other species, and we may roughly say that parental heredity in the species hitherto dealt with is close to .5.

(vi) Fraternal correlation for the physical characters of man dealt with in this memoir is also close to .5. This is in good agreement with the result obtained for eight physical and eight mental characters compared in pairs of brothers in schools. While, however, parental correlations are in good accord for different species, fraternal correlations in such species have a much wider range. This curious result is being further considered, but the tentative suggestion is made that it is due either to different degrees of unit or of intermittent prepotency in the members of these species.

(vii) For the first time in this paper statistics of an extensive kind are given for answering the problems of cross heredity, and an empirical formula is given for determining cross heredity from direct heredity and organic correlations. Some years ago, I proposed for cross heredity a formula which amounted in the notation of the present memoir to

$$r_{1'2'} = \frac{1}{2} (r_{11'} r_{1'2} + r_{22'} r_{12})$$

where 1, 2 are the organs in the first, 1', 2' the like organs in the second relative. This formula was based on a theory involving the constancy of the heredity coefficient for all characters (cf. (v) above). It is shown in the present paper that on the average $\frac{1}{2}$ must be replaced by .57 for parental and by .56 for fraternal cross correlations. With these numbers we obtain from the direct and organic correlations values of the cross heredity coefficients well within the errors of random sampling. Thus at any rate in the case of man, we are in a position to determine cross-heredity for the physical characters without direct investigation. A further research on cross-heredity will, I hope, shortly be published.

(viii) The values of the parental correlations determined for man, show that two or three generations of selection would suffice to raise the mean of the offspring to the selected standard. Further with quite reasonable values of the grandparental correlations no regression would take place, and the stock breed true.

The result is of extreme importance, for two reasons :

(a) It illustrates the absurdity of the prevalent biological conceptions of regression as a constant factor, only restrained by the action of persistent selection.

(b) It emphasises the all-important law that with judicious mating human stock is capable of rapid progress. A few generations suffice to modify a race of men, and the nations which breed freely only from their poorer stocks will not be dominant factors in civilisation by the end of the century.

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