COMPARATIVE INTRAPAIR CORRELATIONS OF FRATERNAL TWINS AND SIBLINGS.

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When Davenport (1920) raised the possibility that the father as well as the mother played a role in the birth of twins (including fraternal twins), the biology of twinning lost somewhat in clarity. Various speculations have been offered in explanation of this phenomenon, which, at first glance, seemed wholly improbable. The hypothesis and its modifications offered by Dahlberg (1926) and Curtius (1927), further developed in the work of Curtius and Verschuer (1932), is perhaps the most radical. Proceeding from the fact, supposedly proven by them, that any twin birth (identical or fraternal) depends on a single recessive gene, and assuming that the roles of father and mother are entirely equal, the latter authors have suggested the following explanation of this phenomenon.

In their opinion, the sperm usually fertilises the secondary oocyte (that is, eggs which have already undergone reduction division). If the fertilisation occurs before equation division, and if a particular gene for twinning ("Teilungsfaktor") enters into the zygote through both the sperm and the egg, then instead of the second polar body there is formed an egg capable of fertilisation. The latter is fertilised by the second sperm. As a result there occur two embryos, which have received a common genotype from the mother, and a different genotype from the father. In the opinion of Curtius and Verschuer such a pair of twins are what we usually call fraternal twins[1] (more properly they might be called "one-and-one-half zygotes"). If, however, fertilisation occurs after the equation division, the homozygotic "Teilungsfaktor" will lead to the further division of the homozygote into two parts, resulting in the birth of identical twins. Thus this hypothesis yields at first glance a clear explanation of two facts noted by different investigators: the part played by the father in the birth of twins, and the greater frequency of births, in comparison with the population, of identical twins in families giving birth to fraternal twins (and *vice versa*). At the same time, should this hypothesis prove correct, we should have to re-examine all conclusions

[1] The authors do not exclude the possibility of the birth of fraternal twins occurring as the result of two ovulations.

drawn from twin research in so far as such conclusions are based on the premise that fraternal twins develop from two usual zygotes, and that intrapair correlations between them are comparable to those which hold for usual pairs of brothers and sisters (the greater resemblance which is sometimes observed between fraternal twins, as compared with brothers and sisters, may be plausibly explained as due to a greater communality of environmental effects, intra-uterine, etc.).

Since the Curtius-Verschuer hypothesis concerns fundamental problems in twin research, we decided to check it. Of the possible ways of verifying it, we have chosen the comparison of intrapair correlation in fraternal twins and in brothers and sisters. We reasoned that, if the hypothesis were really correct, then the intrapair similarity in fraternal twins should be greater than the similarity between one of the twins and his sibling (brother or sister).

Altogether, we investigated 100 pairs of fraternal twins. Simultaneously we examined their brothers and sisters. Five characters were studied: (1) blood groups, (2) taste reaction to para-ethoxyl-phenyl-thio-carbamide (dependent, as is known, on a single pair of genes), (3) colour of the eyes, (4) form of the hair, and (5) lobe of the ear. These were selected as characters least susceptible to age variability. Eye colour was measured on the 12-point scale of Bunak. Hair form was categorised as "straight", "curly", and "wavy". Ear lobes were conditionally graded on a 3-point scale: (1) attached, (2) medium and (3) free. For the several characters we succeeded in testing the following numbers of twin pairs:

Blood groups ...	99 pairs
Taste reaction	68 ,,
Eye colour ...	98 ,,
Hair form ...	87 ,,
Ear lobes ...	95 ,,

The numbers of tested brothers and sisters (other than twins) varied from one to four in the separate families.

In working out the material we proceeded as follows: in each pair of twins we took for reference the firstborn member. With him were compared firstly, his partner, and secondly, that one of the siblings which was nearest in age to the twins. The majority of the siblings were older than their respective twin pairs, and in order to avoid the influence of age (which might, for instance, affect the eye-colour correlation), we compared the firstborn twin with a younger sibling whenever possible. These comparisons were in the minority however. In what follows, we shall always compare fraternal twins with pairs of "twin siblings".

Table I presents certain results in which for each of the five characters is presented the number of cases of intrapair similarity among the twins and among the twin siblings. It is to be noted that similarity by this method is recorded independently of the quality of the results of the study of each pair: that is, with respect to blood groups, a pair is reckoned to be similar when both members belong to group I (II, III or IV); for eye colour, a pair is considered similar when its members show the same number (independently of intensity), and so forth.

TABLE I.

Absolute frequencies of similarity of twins and twin siblings.

	Similar pairs		
	(*a*) Twins	(*b*) Twin siblings	All pairs
Blood groups	56	58	99
Taste reaction	52	49	68
Eye colour	31	26	98
Hair form	57	64	87
Ear lobes	51	47	95

Table I shows that there is generally great coincidence in the frequency of intrapair similarity in pairs of fraternal twins and twin siblings. There is clearly little tendency towards greater similarity in the first class: for three characters the frequency of similarity is greater among the twins, and for two characters the reverse holds. If for eye colour we should refer to a more or less notable prevalence of similarity in twins (31 and 26), it is compensated for in inverse proportion in respect to hair form (57 cases of similarity in twin pairs and 64 in twin siblings).

It may already be concluded from the above data that the hypothesis of Curtius and Verschuer is incorrect. We have, however, further data illustrating the same thing. In so far as two of the five characters (eye colour and ear lobes) are quantitative, we have calculated the average intrapair differences in them for the two sibling categories at hand. The results are shown in Table II.

TABLE II.

Average intrapair differences in eye colour and ear lobes.

Kind of pairs	Function	Average intrapair differences
Fraternal twins	Eye colour	2·00
Pairs of twin siblings	,, ,,	2·10
Fraternal twins	Ear lobes	0·43
Pairs of twin siblings	,, ,,	0·51

In Table II are seen almost identical figures, and they are in accord with the results of Table I.

Finally, making use of the fact that two of the above functions (blood groups, and taste reaction to phenyl-thio-carbamide) are determined by proper genes, we calculated the theoretically expected frequencies of the different classes in a fraternal correlation table and compared them with obtained results. For taste reaction we made use of the well-known table concerning monofactorial segregation (Table III).

TABLE III.

Association of siblings in monohybrid traits.

	AA	Aa	aa	
AA	$p^2(p+\frac{1}{2}q)^2$	$p^2q(p+\frac{1}{2}q)$	$\frac{1}{4}p^2q^2$	p^2
Aa	$p^2q(p+\frac{1}{2}q)$	$pq(1+pq)$	$pq^2(\frac{1}{2}p+q)$	$2pq$
aa	$\frac{1}{4}p^2q^2$	$pq^2(\frac{1}{2}p+q)$	$q^2(\frac{1}{2}p+q)$	q^2
	p^2	$2pq$	q^2	

For the blood groups we arranged an association table based on the assumption of three allelomorphs (Table IV).[1]

TABLE IV.

Association of siblings for functions determined by three gene allelomorphs.

	OO	AA	AO	BB	BO	AB	
OO	$\frac{1}{4}r^2(1+r)^2$	$\frac{1}{4}p^2r^2$	$\frac{1}{2}pr^2(1+r)$	$\frac{1}{4}q^2r^2$	$\frac{1}{2}qr^2(1+r)$	$\frac{1}{2}pqr^2$	r^2
AA	$\frac{1}{4}p^2r^2$	$\frac{1}{4}p^2(1+p)^2$	$\frac{1}{2}p^2r(1+p)$	$\frac{1}{4}p^2q^2$	$\frac{1}{2}p^2qr$	$\frac{1}{2}p^2q(1+p)$	p^2
AO	$\frac{1}{2}pr^2(1+r)$	$\frac{1}{2}p^2r(1+p)$	$\frac{1}{2}pr(2+2pr-q)$	$\frac{1}{2}pq^2r$	$\frac{1}{2}pqr(1+2r)$	$\frac{1}{2}pqr(1+2p)$	$2pr$
BB	$\frac{1}{4}q^2r^2$	$\frac{1}{4}p^2q^2$	$\frac{1}{2}pq^2r$	$\frac{1}{4}q^2(1+q)^2$	$\frac{1}{2}q^2r(1+q)$	$\frac{1}{2}pq^2(1+q)$	q^2
BO	$\frac{1}{2}qr^2(1+r)$	$\frac{1}{2}p^2qr$	$\frac{1}{2}pqr(1+2r)$	$\frac{1}{2}q^2r(1+q)$	$\frac{1}{2}qr(2+2qr-p)$	$\frac{1}{2}pqr(1+2q)$	$2qr$
AB	$\frac{1}{2}pqr^2$	$\frac{1}{2}p^2q(1+p)$	$\frac{1}{2}pqr(1+2p)$	$\frac{1}{2}pq^2(1+q)$	$\frac{1}{2}pqr(1+2q)$	$\frac{1}{2}pq(2+2pq-r)$	$2pq$
	r^2	p^2	$2pr$	q^2	$2qr$	$2pq$	

The corresponding concentrations of genes (p and q for taste reactions, and p, q and r for blood groups) were calculated separately for fraternal twin pairs and for twin-sibling pairs, from the data in hand. Because the concentrations of these genes are different among different racial groups, our calculations were made separately for Russian pairs, which constitute the largest part of our material, and for all pairs taken together. This seemed admissible, since, as is seen in the following tables, the respective concentrations of genes differ little from each other, probably as a result of the great prevalence of Russians in our material.

[1] Here and further we refer provisionally to three alleles, since groups A_1 and A_2 had not been distinguished. It will be understood, however, that this combining of the two into the A group has no effect on our calculations.

Using the Tables III and IV and the corresponding concentrations of the genes, we calculated the theoretically expected figures for each group. These are represented by the upper figures in Tables V–XII, while the lower figures are the obtained results. For example: we find that in the total twin population (Table X), the proportion of persons in blood group I (sum of the figures in column *OO*, Table IV) equals 0·422 (r, concentration of the recessive gene in this population, 0·65). This proportion evidently is the same for their siblings, on the supposition that each person has one sibling. The proportion of siblings of persons in group I who are also of group I is represented by the expression $\frac{1}{4}r^2\,(1+r)^2$, in this case equal to 0·287. It follows that of all the siblings of persons of group I, 0·681 (=287/422) will belong to group I.

In so far as all the first partners of blood group I amounted to 39, it is clear that group I siblings must be $39 \times 0{\cdot}681 = 26{\cdot}559$.

All the remaining calculations have been made in this manner.

It is necessary to add that the probability that the assumed hypothesis is correct (*P*) has been calculated in Tables V–XII by the χ^2 method. In view of the fewness of cases, persons in blood groups II and IV have been thrown together in Tables IX–XII. It is also understood that in constructing Tables V–XII we threw together different genotypes having similar phenotypical expressions. In Tables V–VIII are all persons giving positive taste reactions, that is, *AA* and *Aa*, and in Tables IX–XII are thrown together *AO* and *AA*, *BO* and *BB*. As a result we have in Tables V–VIII four classes instead of the nine shown in Table III; in Tables IX–XII are nine rather than the 36 classes of Table IV. All the results obtained, as well as the corresponding χ^2 and probabilities (*P*), are presented in Tables V–XII.

TABLE V.

Taste reactions. Russian twins, 53 pairs.

	Tasters	Non-tasters
Tasters	22·5	7·1
	22·0	5·0
Non-tasters	7·5	15·9
	8·0	18·0

$p=0{\cdot}33,\quad q=0{\cdot}67,\quad \chi^2=1{\cdot}24,\quad P=0{\cdot}27.$

TABLE VI.

Taste reactions. All twins, 68 pairs.

	Tasters	Non-tasters
Tasters	31·20	8·68
	30·00	7·00
Non-tasters	8·80	19·32
	10·00	21·00

$p=0{\cdot}34,\quad q=0{\cdot}66,\quad \chi^2=0{\cdot}67,\quad P=0{\cdot}44.$

TABLE VII.

Taste reactions. Russian twin siblings, 52 *pairs.*

	Tasters	Non-tasters
Tasters	22·04	7·13
	23·00	7·00
Non-tasters	6·96	15·87
	6·00	16·00

$p=0{\cdot}34$, $q=0{\cdot}66$, $\chi^2=0{\cdot}17$, $P=0{\cdot}69$.

TABLE VIII.

Taste reactions. All twin siblings, 66 *pairs.*

	Tasters	Non-tasters
Tasters	29·64	9·24
	29·00	10·00
Non tasters	8·36	18·76
	9·00	18·00

$p=0{\cdot}37$, $q=0{\cdot}63$, $\chi^2=0{\cdot}19$, $P=0{\cdot}67$.

TABLE IX.

Blood groups. Russian twins, 80 *pairs.*

	I	II+IV	III
I	18·27	5·15	5·28
	13·00	6·00	8·00
II+IV	6·38	18·55	5·28
	10·00	19·00	5·00
III	4·35	3·30	13·44
	6·00	2·00	11·00

$p=0{\cdot}23$, $q=0{\cdot}18$, $r=0{\cdot}59$, $\chi^2=6{\cdot}71$, $P=0{\cdot}16$.

TABLE X.

Blood groups. All twins, 99 *pairs.*

	I	II+IV	III
I	26·13	7·17	6·24
	21·00	6·00	9·00
II+IV	8·19	23·36	4·94
	11·00	26·00	5·00
III	4·68	3·18	14·30
	7·00	2·00	12·00

$p=0{\cdot}21$, $q=0{\cdot}14$, $r=0{\cdot}65$, $\chi^2=5{\cdot}61$, $P=0{\cdot}23$.

TABLE XI.

Blood groups. Russian twin siblings, 80 *pairs.*

	I	II+IV	III
I	18·85	5·69	5·52
	18·00	5·00	11·00
II+IV	6·09	18·32	4·80
	5·00	20·00	3·00
III	4·06	3·03	13·44
	6·00	2·00	10·00

$p=0{\cdot}22$, $q=0{\cdot}16$, $r=0{\cdot}62$, $\chi^2=8{\cdot}75$, $P=0{\cdot}07$.

TABLE XII.

Blood groups. All twin siblings, 99 *pairs.*

	I	II+IV	III
I	26·559	7·639	6·552
	26·000	6·000	12·000
II+IV	7·371	22·650	4·836
	7·000	25·000	3·000
III	4·992	3·677	14·560
	6·000	3·000	11·000

$p=0{\cdot}20$, $q=0{\cdot}15$, $r=0{\cdot}65$, $\chi^2=7{\cdot}047$, $P=0{\cdot}14$.

These tables reveal the fact that the probabilities of correctness (P) of the assumed hypotheses concerning monofactorial segregation of taste reactions and triple allelomorphs for blood groups are everywhere real (the lower limit of certainty by the χ^2 method is 0·05). Comparing the results obtained for the twin pairs with the results for twin siblings, it is seen that for taste reactions the probability of correctness of the assumed hypotheses is higher for twin siblings than for twins (0·69 and 0·67 for the former, and 0·27 and 0·44 for the latter). At the same time, the reverse holds in respect to blood groups (0·07 and 0·14 for twin siblings, and 0·16 and 0·23 for twins). This leads us to believe that the differences obtained are due to chance, and that on the whole it should be recognised that intrapair correlations in fraternal twins for these two characters determined by proper genes correspond to the correlations expected on the assumption that fraternal twins differ genotypically not less than ordinary siblings. It is interesting to note that Verschuer himself, collaborating with Schiff (1931, 1933) and using another method, also concluded that for blood groups, for genes M and N and for certain other genes, the similarity of fraternal twins does not differ from the similarity of siblings.

The results enable us to draw the following conclusions:

(1) There is no basis for assuming the hypothesis of Curtius and Verschuer concerning the biology of twinning. Intrapair correlations studied by different methods in pairs of fraternal twins and in pairs of twin siblings, give no reason whatever for affirming a greater genotypical likeness for fraternal twins than for usual siblings.

(2) It follows that in case a higher intrapair correlation is reported for fraternal twins than for siblings, such a difference is attributable to the influence of exogenous factors, to the greater environmental communality of fraternal twins as compared with that of brothers and sisters.[1]

[1] The possibility is not excluded that the first division may sometimes be equational (see for instance Goldschmidt, Mather, etc.). But this would hardly disturb our conclusions because it would not hold for *all* the genes determining the characters here considered, unless we made the very improbable assumption (1) that the first division was equational

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for all the other chromosomes even though it was shown by Painter not to be so for the *X*-*Y* pair, and (2) that there is no crossing-over in man, for crossing-over results in genes not near the spindle fibre often undergoing reduction during the division that is equational for the spindle-fibre locus.

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