

THE GENESIS OF TWINS

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In 1905 an investigation of the resemblance which exists between twins, was carried out by EDWARD L. THORNDIKE (1905) of COLUMBIA UNIVERSITY. The work was well designed to elucidate the extent and the nature of the resemblance between twins of school age, both in mind and body. Nevertheless the results differ so widely from expectation upon the current theories of heredity and the genesis of twins, that they have not been incorporated among the generally recognized facts of inheritance. It is proposed to examine the results from this point of view, and to suggest a theory of the genesis of twins which appears to reconcile the differences.

The correlations found in six mental traits range from .69 to .90 with a standard error of about $\pm .05$, while the eight physical traits range from .71 to .86 with a standard error $\pm .06$. There is thus a considerable degree of agreement between different traits, and a general level of correlation not far from .80. This is an astonishingly high value. Fraternal resemblance is usually not far from .54, so that 46 percent of the variance of the population occurs within the sibship; according to these figures, variance within the twinship must be rather less than half this quantity.

Upon the supposition that some of the twins are related fraternally and some are identical, the latter contributing little or nothing to the variance, at least half of the 50 pairs of twins covered by this investigation must be identical twins. This suggestion is supported by the distribution of the sexes, for out of 50 pairs of twins only 9 are of different sexes. Nevertheless it is quite incompatible with the actual figures, as THORNDIKE has shown under the heading "Specialization of resemblance."

It is impossible to pick out any pair of twins, much less any large group of twins, which resemble each other closely in all features. But we can go further than this. The variable used by THORNDIKE, to

measure the resemblance between any pair of twins in any factor is r where

$$r = \frac{2xy}{x^2 + y^2}$$

and x and y are the deviations of the two twins.

When x and y are the coordinates of a point on a plane, r is constant along any line passing through the origin, that is along any diameter of the frequency distribution. If θ is the angle between this diameter and either axis the distribution of the values of r may thus be used to investigate the frequency surface.

The distribution of the observed values of r is peculiar; there are concentrations at both extremes, especially near to $+1$; of 234 values derived from 39 pairs of twins for 6 physical traits, no less than 102 are above .895, and of these 27 exceed .995. THORNDIKE suggests that the form of distribution of twin resemblance is a unimodal curve comparable with that for the number of children in different families, but in this he overlooks the effects of sampling.

For a perfectly homogeneous, normally correlated population, the chance of any observation falling within the range $dx dy$ is

$$df = \frac{1}{2\pi\sigma^2\sqrt{1-\rho^2}} e^{-\frac{x^2 - 2\rho xy + y^2}{2\sigma^2(1-\rho^2)}} s^2 dx dy$$

where ρ is the correlation. If s be the distance from the centre, and θ the angle the radius makes with the axis of x , then

$$x = s \cos \theta, y = s \sin \theta$$

$$dx dy = s d\theta ds$$

and

$$df = \frac{1}{2\pi\sigma^2\sqrt{1-\rho^2}} e^{-\frac{1-\rho \sin 2\theta}{2\sigma^2(1-\rho^2)} s^2} s ds d\theta;$$

remembering that $\sin 2\theta = r$, and $d\theta = \frac{dr}{2\sqrt{1-r^2}}$

it follows that

$$df = \frac{1}{2\pi\sigma^2\sqrt{1-\rho^2}} e^{-\frac{1-\rho r}{1-\rho^2} \cdot \frac{s^2}{2\sigma^2}} s ds \cdot \frac{dr}{2\sqrt{1-r^2}}.$$

On integrating this expression with respect to s from 0 to ∞ the frequency within the elemental sector dr is

$$\frac{1}{2\pi\sigma^2\sqrt{1-\rho^2}} \cdot \frac{\sigma^2(1-\rho^2)}{1-\rho r} \cdot \frac{dr}{2\sqrt{1-r^2}};$$

but four equal elemental sectors have the same r ; so that the frequency of a random sample falling within the range dr is

$$\frac{\sqrt{1-\rho^2}}{\pi} \cdot \frac{dr}{(1-\rho r)\sqrt{1-r^2}}$$

This expression specifies the curve of random sampling: by integrating with respect to r we obtain for the frequency of samples less than r , the expression

$$f = \frac{2}{\pi} \tan^{-1} \sqrt{\frac{1-\rho}{1+\rho} \cdot \frac{1+r}{1-r}}$$

As soon as we examine the curve it is evident that it agrees well with the observed values of r . The ordinate becomes infinite at ± 1 , thus explaining the concentrations at the extremes, there is no mode, but the expression for the probability integral shows that the median ($f = 1/2$), is at $r = \rho$. This is a sufficient guide in fitting the curve to the observed data. The medians for the 6 traits range from .80 to .88, and the median of the whole group is .85,

In order to test the agreement between this curve and the observed values, the sextiles are calculated from the probability integral and the range thus divided into six divisions of equal frequency; the results are shown in table 1.

P , the chance of a worse fit by random sampling, being .46, the distribution of the values of r is satisfactorily explained as being due solely to chance. It is likely, then, that the twins form a homogeneous group, with the correlations of the physical traits all not far from .85.

To make a more thorough test of homogeneity it is necessary to determine whether there is any correlation between the resemblances of the same pair of twins in different traits. For this purpose the variable r is not suitable. Its curve of distribution is far from normal and the end of its range is so cramped that 12 percent of the observations fall into one four-hundredth of the range. In addition the curve changes its form rapidly as ρ is altered, and since we are examining the possibility that different pairs of twins are samples corresponding to different values of ρ , it is essential, if the correlation is to be at all intelligible, that the

TABLE I¹

Sextiles $\rho = .85$	Frequency	Frequency observed	Difference	d^2
- 1.000				
- .661	39	35	-4	16
+ .609	39	47	+8	64
+ .850	39	36	-3	9
+ .947	39	31	-8	64
+ .9884	39	44	+5	25
+ 1.0000	39	41	+2	4
	$\chi^2 = 4.67$		$P = .46$	
				Total 182

¹ In this table THORNDIKE'S figures are used without correction; a more complete test, using the corrected figures divided into thirteen groups, gives an even higher value, $P = .701$.

curve, though varying in position, should be approximately constant in form.

It so happens that the distribution

$$df = \frac{\sqrt{1 - \rho^2}}{\pi} \cdot \frac{dr}{(1 - \rho r)\sqrt{1 - r^2}}$$

is capable of a transformation which precisely fulfills these conditions, for writing $2z = \log \frac{1 + r}{1 - r}$, that is, $r = \tanh z$ and $\rho = \tanh \zeta$ we have

$$df = \frac{1}{\pi} \operatorname{sech}(z - \zeta) dz$$

a curve symmetrical about the centre, ζ , and falling off exponentially when $(z - \zeta)$ is large (figure 1).

The observed values of z may be found either from those of r , or as is desirable for high values, directly from the observations, for if x and

y are the two measurements, $z = \log_e \frac{x + y}{x - y}$. There remain a few cases

in which the measurements are identical, and z nominally infinite, but a consideration of the units in which the measurements are made, and of the manner in which the probability of any assigned value of z falls off when $z - \zeta$ is large, is sufficient to restrict the value of z , with fair

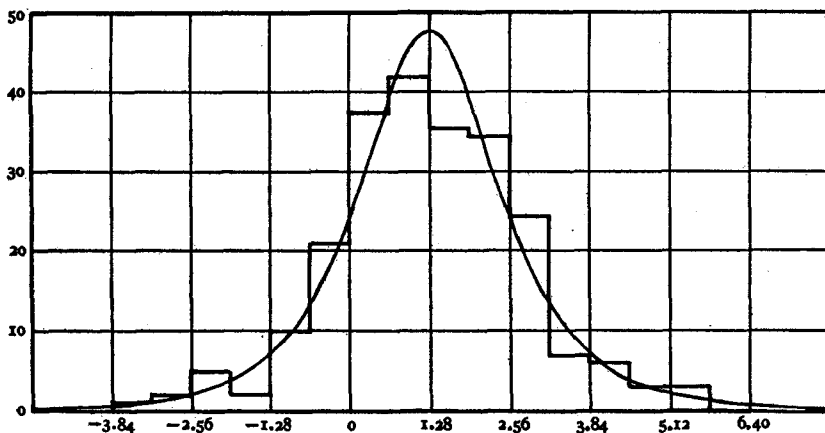


FIGURE 1

probability to sufficiently narrow limits. The figures obtained in this way are given in table 2.

When the resemblances have been expressed in terms of the new variable, a correlation table may be constructed by picking out every pair of resemblances between the same twins in different traits. The values are now centered symmetrically about a mean at 1.28, and the correlation is found to be $-.016 \pm .048$, negative but quite insignificant. The result entirely corroborates THORNDIKE'S conclusions as to the specialization of resemblance; it further shows that in the population here considered, there are neither discontinuous nor continuous gradations of similarity; the population is strictly homogeneous.

The mean value 1.28, corresponds to $\rho = .856$. The transformation has not however, been made in order to determine the mean resemblance, but to test the homogeneity of the population. The value of the correlation which best fits the data may be found with less probable error, from the product-moment correlations; the mean of the values given by THORNDIKE is .79, and this value is to be preferred to the other. The differences in the mean resemblances of the six traits taken separately, are not statistically significant.

Another way of examining the distribution of resemblance is to take the means of the 6 transformed resemblances for each pair of twins. In figure 2 is shown the distribution of the 39 means, together with the curve of distribution on the supposition of uniform origin. The shape and width of this curve do not depend on the position of its centre; in the figure it is centred on the actual mean of the resemblances, 1.28.

TABLE 2

	Height	Height sitting	H/H.S.	Head circumference	Head width	Cephalic index	Total	Mean
1	2.45	4.80	1.10	2.10	1.25	3.18	14.88	2.48
2	.13	2.52	2.76	1.79	2.01	2.34	11.55	1.93
5	.64	.75	.25	2.56	1.61	.12	5.93	.99
6	— .16	1.61	2.20	2.83	.08	.47	7.03	1.17
7	.03	— .88	3.81	0	— .22	1.61	4.35	.72
8	2.07	1.82	1.45	1.39	1.19	2.66	10.58	1.76
9	.75	2.05	—1.61	— .74	2.83	2.02	5.30	.88
10	1.82	1.65	2.57	3.04	1.05	.57	10.70	1.78
11	— .09	.89	3.93	0	2.92	3.02	10.67	1.78
12	.26	2.20	2.03	1.16	2.40	.46	8.51	1.42
13	.99	.14	.17	— .69	1.35	.44	2.40	.40
16	.43	—1.22	— .30	2.17	1.39	3.89	6.36	1.06
17	1.47	2.83	2.06	1.85	2.30	1.79	12.30	2.05
18	1.24	1.26	0	.51	— .41	3.72	6.32	1.05
19	2.80	3.25	2.20	4.39	— .16	—1.44	11.04	1.84
20	1.90	4.32	— .14	0	2.48	2.63	11.19	1.86
21	0	.86	0	.87	1.89	2.80	6.42	1.07
23	5.41	2.71	2.71	.41	—2.17	— .89	8.18	1.36
24	.93	2.40	0	—1.95	.69	2.37	4.44	.74
25	2.86	.37	—1.95	1.03	2.71	.73	5.75	.96
26	4.10	3.64	1.61	1.36	.47	1.24	12.42	2.07
27	.36	1.85	.88	2.51	3.29	2.24	11.13	1.85
28	1.01	1.49	5.03	—1.10	2.40	— .16	8.67	1.44
29	.35	— .26	—3.22	— .51	.67	.93	—2.04	— .34
30	5.14	.99	1.39	.29	1.39	.14	9.34	1.56
31	1.12	.96	2.20	1.77	3.00	1.39	10.44	1.74
32	—1.10	2.50	1.81	2.89	2.20	.85	9.15	1.53
34	1.34	.51	— .13	.69	2.25	1.47	6.13	1.02
35	2.70	4.27	1.73	1.69	1.39	— .24	11.54	1.92
36	3.13	3.56	2.46	—2.17	.34	—2.67	4.65	.77
37	1.97	.62	1.25	1.10	0	.47	5.41	.90
38	1.28	.93	1.95	.34	—2.89	.93	2.54	.42
40	— .46	—2.30	.74	5.45	0	—1.21	2.22	.37
41	—1.22	— .11	.57	.92	1.95	2.23	4.34	.72
43	— .24	.37	4.50	1.61	3.45	2.94	12.63	2.10
44	.89	.14	.45	1.22	1.82	—1.05	3.47	.58
45	2.20	.92	1.69	1.10	.59	1.10	7.60	1.27
47	1.86	2.75	0	2.20	.69	2.11	9.61	1.60
50	1.50	— .07	.46	1.10	1.10	3.18	7.27	1.21
Total	51.86	57.09	48.61	45.18	49.30	48.38	300.42	
Mean	1.33	1.46	1.25	1.16	1.26	1.24		1.284

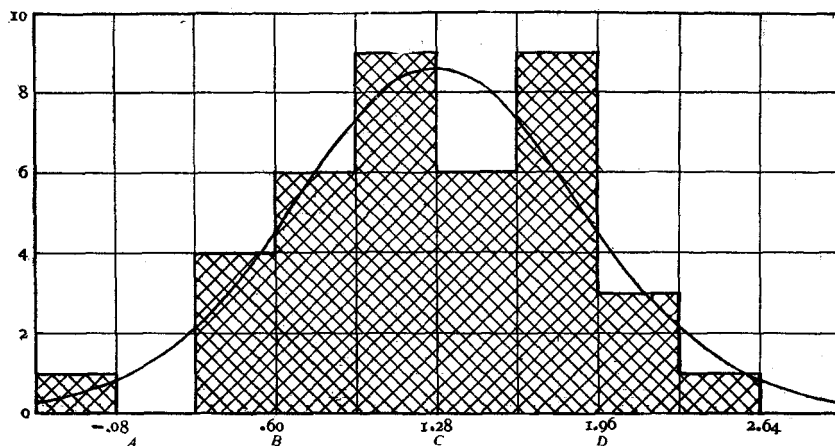


FIGURE 2

For unrelated children the curve would be centered at A ($\rho = 0$), for brothers we should expect it to be near B ($\rho = .54$), and for identical twins not far from D ($\rho = .96$); the conclusion that the origin of twins is uniform, which we have drawn from the absence of correlation between the resemblances of the same pair, is equally demonstrable from the distribution of the means. If, for instance, it were supposed that some of the twins were of fraternal origin, we should expect half of these to lie above and half below the point B. As a fact only 5 in all lie below B, so that we cannot reasonably suppose that more than 10 are of fraternal origin. Exactly the same argument shows that not more than 8 are identical twins, leaving at least 21 pairs to be accounted for by some new hypothesis. But in taking away the 9 extreme values as fraternal or identical twins, we have left the remainder with a variance considerably less than that to be expected from chance alone. There is in fact no excess at the extremes to be disposed of: the group is apparently quite homogeneous.

The same conclusion follows if we consider the 8 pairs of twins of different sexes. These must supposedly all be fraternal twins; but only one of them lies below B. The mean is at 1.04, corresponding to $\rho = .78$, slightly lower than the general average, but not unreasonably so for such a small sample, even if the different rates of development of boys and girls leaves the figures strictly comparable. The results are certainly unfavorable to the view that these twins are fraternal.

Both curves fit the data exceptionally well. For the distribution of all

resemblances (figure 1) the chance of a worse fit by random sampling is .701; for the distribution of mean resemblances (figure 2) it is .745.

The fact that the observations examined critically show themselves to be a strictly homogeneous population, with correlation much larger than that between sibs, requires a new theory of the genetic connection between twins. It is here suggested that the facts may be explained by the supposition that twins ordinarily share the hereditary nature of one gamete but not of the other.

This theory may be tested by the methods explained in a recent paper, (FISHER 1919). If the alternative types of gamete of any Mendelian character occur in the ratio $p:q$, then a pair of twins will exhibit different combinations of the three possible phases, with the frequencies shown in table 3.

TABLE 3
First Twin

Second twin	Dominant	Heterozygous	Recessive
Dominant	$p^2(p + \frac{1}{2}q)$	$\frac{1}{2} p^2 q$	
Heterozygous	$\frac{1}{2} p^2 q$	$3/2 pq(p + q)$	$\frac{1}{2} pq^2$
Recessive		$\frac{1}{2} q^2 p$	$q^2(\frac{1}{2}p + q)$

If $i, j,$ and k are the deviations from the mean corresponding to the three phases, the contribution of this phase to the product-moment of pairs of twins must therefore be

$$p^2(p + \frac{1}{2}q)i^2 + p^2 q i j + 3/2 pq(p + q)j^2 + pq^2 j k + q^2(\frac{1}{2}p + q)k^2$$

and this reduces to $\frac{3}{4} \beta^2 + \frac{1}{2} \delta^2$ where β^2 is that portion of variance due to this factor which is regularly inherited, and δ^2 is the remainder due to dominance. If mating were at random, then, the correlation between twins would be

$$\frac{3}{4} \frac{\tau^2}{\sigma^2} + \frac{1}{2} \frac{\epsilon^2}{\sigma^2},$$

where τ^2 and ϵ^2 are the totals of the elements β^2 and δ^2 contributed by the different Mendelian factors, and σ^2 is the sum of τ^2 and ϵ^2 . This may be compared to the value found for the fraternal correlation,

$$\frac{1}{2} \frac{\tau^2}{\sigma^2} + \frac{1}{4} \frac{\epsilon^2}{\sigma^2},$$

and for the paternal correlation

$$\frac{1}{2} \frac{\tau^2}{\sigma^2}$$

upon the same assumptions.

Neglecting environment, and which is far more important, assortative mating, we should have

$$t = 2f - \frac{1}{2} p$$

where t , f , and p are the correlation between twins, the fraternal and the parental correlations.

As a preliminary test we may take the figures for stature

$$f = .5433, \quad p = .5066,$$

whence

$$t = .8300,$$

a result evidently about the right magnitude.

It would not be correct to be satisfied with this verification, for the values of the fraternal and parental correlation could not be so high as they are if mating were at random. It will be found, however, that assortative mating affects these correlations nearly proportionally.

Following the methods before alluded to, it may be shown that

$$t = \frac{c_1}{4} (3 + c_2 A)$$

where c_1 and c_2 are reduction factors for environment and dominance respectively, and A the genetic association due to assortative mating.

The correlation between husband and wife is probably due to two distinct causes, the relative importance of which differs in different traits. If it were due to direct selection, which is probably the principal cause in the case of stature, we arrive at the formula

$$t = 3f - \frac{3}{2} \frac{p}{1 + \mu} - \frac{5 p^2 \mu}{(1 + \mu)^2}$$

where μ is the marital correlation. Taking $\mu = .2804$, this gives $t = .818$.

If on the other hand the marital correlation be due to indirect selection, as is apparently the case with span, we have

$$t = 3f - \frac{3}{2} p - \frac{1}{2} \mu;$$

substituting the values for span, $\mu = .1989$, $p = .4541$, $f = .5351$, we obtain

$$t = .825.$$

Evidently the agreement with the actual observations is extremely close.

The theory of the genesis of twins suggested above is in accordance with the well known fact that the father plays an important part in the causation of twinning. If the twins were formed from separate ova, fertilized by two different spermatozoa, it is difficult to see in what manner the father could influence their production. In the supposed case of identical twins formed by the division of a single zygote, the

tendency of the zygote to divide should indeed be inherited equally from either parent, but it is not easy to believe that in all the instances of paternal influence we are concerned with identical twins.

In an instance given by WAKLEY² (1895), of two twin brothers, one has a pair of twin sons, and five singly born children, the other one son; the former has through his sons three pairs of twin grandchildren, at least one pair being of opposite sex; the latter one pair of twin granddaughters. In this case a tendency to twinning, but not necessarily identical twinning, is carried by the fathers.

If we suppose that in certain cases the ovum after maturation is induced to divide into two identical portions, which are fertilized by different spermatazoa, not only is the observed resemblance of twins numerically explained, but the influence of the father is open to reasonable explanation. The division of the ovum presumably takes place during fertilization, under the direct influence of the two spermatazoa.

DAVENPORT mentions that besides the families in which the twinning tendency is carried by the males, there are other families in which it is inherited in the female line. The theory here put forward requires that the male and female gametes should be required to play different parts in the formation of twins, and the existence of two heritable qualities, the one affecting males, and the other females, is a definite confirmation of the theory.

The facts regarding the sex of twins are also in agreement with the above theory. It is generally agreed that sex in man is determined by the spermatozoon, so that the identity of the ovum does not necessitate identity of sex. The preponderance of twins of like sex, does indeed become a new problem, because it has been formerly believed to be due to the proportion of identical twins. So far as I am aware, however, no attempt has been made to show that twins are sufficiently alike to be regarded as identical really exist in sufficient numbers to explain the proportion of twins of like sex.

At least two circumstances do suggest that twins should be more often than not of like sex. For an ovum to divide and unite with two spermatazoa, instead of normally with one, it would seem to be essential that the spermatazoa should enter simultaneously and prepare themselves for union with equal speed. It may be that the necessary equipoise of attractive forces is more likely to be maintained between spermatazoa of like sex than between those of unlike sex.

In the second place much evidence has been adduced, for example by HERTWIG (1912) in the case of frogs, and by PEARL and PARSHLEY

(1913) in that of cattle, that ripeness of the ovum at fertilization is a factor in sex determination. This belief is not opposed to belief in the determination of sex by the spermatozoa, since it is possible that ova at various stages of ripeness exert selection among the gametes about to fertilize them. If, however, this belief in the effects of ripeness is well founded, it would explain why ova of the same age should tend on the whole to develop like sexes. On the other hand, if ripeness is an important factor, twins formed from different ova, and these must be upon the existing theory the majority of twins, should be generally of opposite sex, since ova simultaneously available for fertilization would ordinarily differ much in ripeness.

We may conclude then, that of the ascertainable facts concerning twins, the measurable degree of resemblance, the existence of paternal influence, the inheritance of male and female tendencies to twinning, all favor the supposition as to the origin of ordinary twins here set forth, while the distribution of sex in pairs of twins appears to present no serious difficulties.

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