The Heritability of Certain Anthropometric Characters as Ascertained from Measurements of Twins

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INTRODUCTION

VARIATION in some of the most interesting human attributes is of a nearly continuous nature and has not yet been associated with specific genes. For this reason there is sometimes disagreement concerning the relative importance of environmental and genetic factors in producing this variation. Estimates of the genetic component of the variation which are based on sib-sib and parent-offspring correlation or regression tend to be exaggerated by the fact that environmental factors are not constant between families. The unique advantage of twins in overcoming this difficulty has been recognized since the time of Galton. Until recently, however, the number of recognizable and commonly variable genetic characters has been too small to be of much use in diagnosing zygosity. Partly for this reason and partly because of the expense of obtaining extensive data from series of twins not many comprehensive studies of heritability have been attempted with them.

In 1952 the Institute of Human Biology, under the direction of Lee R. Dice, initiated the Hereditary Abilities Study with the purpose of investigating the heritability and interrelationships of a number of psychological, biochemical, and physical traits. The data collected by this study consist of numerous measurements from monozygous and like-sexed dizygous twins. The present paper, which is concerned with the heritability of the physical traits only, is one of a series of reports which will be based on these data.

CHARACTERS STUDIED

The anthropometric traits investigated were selected with the advice of J. N. Spuhler and are listed in Table I. The definitions of most of these characters and the methods employed in making the measurements are those of Martin (1928). The numbers by which Martin designated these traits are given in Table I. Martin does not describe bicondylar breadth of the arm, but this measurement is wholly analogous to bicondylar breadth of the leg. The dermatoglyphic traits—finger print pattern intensity and palmar main-line index—are described by Cummins and Midlo (1943). The data on birth weights were obtained from parent interviews. For bilateral characters the mean of the measurements from both sides was used as the value of the trait for each individual.

TABLE I. MARTIN NUMBERS AND ESTIMATES OF THE VARIANCE WITHIN LIKE-SEXED DIZYGOUS TWINS, σ_D^2, THE VARIANCE WITHIN MONOZYGOUS TWINS, σ_M^2, AND OF HERITABILITY, h^2, FOR VARIOUS ANTHROPOMETRIC TRAITS

Traits	Martin Numbers	σ_D^2	σ_M^2	$h^2 \times 100$
Birth weight, oz		78.9	51.1	35
Current weight, lbs		134.1	41.4	69**
Stature, mm	1	1620.3	195.4	88**
Span, mm	17	2132.0	317.7	85**
Sitting height, mm	23	462.8	130.7	72**
Bi-iliac breadth, mm	40	195.0	79.0	59**
Total arm length, mm	45	525.2	54.0	90**
Forearm length, mm	48	67.3	12.9	81**
Hand length, mm	49	21.3	3.9	82**
Middle finger length, mm	51	11.9	1.4	88**
Hand breadth, mm	52	8.7	1.7	80**
Bi-acromial breadth, mm	55	154.6	106.7	31
Foot length, mm	58	58.5	10.9	81**
Chest circumference, mm	61	1098.8	423.7	61**
Waist circumference, mm	62	1300.8	978.8	25
Neck circumference, mm	63	174.1	57.1	67**
Hip circumference, mm	64	16.1	6.0	63**
Midarm circumference, mm	65	301.5	114.0	62**
Forearm circumference, mm	66	103.0	48.7	53**
Wrist circumference, mm	67	23.3	8.2	65**
Bicondylar breadth—leg, mm	68(4)	21.0	8.2	61**
Bicondylar breadth—arm, mm		11.9	3.5	71**
Maximum calf circumference, mm	69	341.9	84.8	75**
Minimum ankle circumference, mm	70	63.9	29.3	54**
Head length, mm	1	20.9	9.6	54**
Head breadth, mm	3	14.9	4.2	72**
Minimum frontal breadth, mm	4	6.1	2.4	61**
Bi-zygomatic breadth, mm	6	8.8	3.5	60**
Bi-gonial breadth, mm	8	13.2	3.8	71**
Interpalpebral breadth, mm	9	4.5	1.8	60**
Bi-palpebral breadth, mm	10	6.1	3.6	41*
Interpupillary distance, mm	12	5.6	1.7	70**
Nose breadth, mm	13	3.2	1.1	66**
Head height, mm	15	27.7	8.7	69**
Total facial height, mm	18	20.0	5.3	74**
Upper facial height, mm	20	11.4	3.2	72**
Nose height, mm	21	9.3	2.2	76**
Ear height, mm	29	4.8	1.2	75**
Ear breadth, mm	30	2.9	1.4	52*
Head circumference, mm	45	100.0	26.1	74**
Cephalic module, mm		10.3	2.1	80**
Cephalic index × 100		7.1	4.4	38
Cephalo-facial index × 100		5.7	2.6	54**
Total facial index × 100		14.5	4.0	72**
Relative shoulder breadth × 100		0.6	0.4	33
Relative sitting height × 100		0.9	0.3	67**
Reciprocal ponderal index		90.5	26.5	71**
Fingerprint pattern intensity		9.1	1.1	88**
Palmar main-line index		7.7	3.0	61**

* Significant at the 5% level.
** Significant at the 1% level.

The ratios studied are defined as follows:
  Cephalic index: head breadth/head length
  Cephalo-facial index: bi-zygomatic breadth/head breadth
  Cephalic module: (head height + head length + head breadth)/3
  Total facial index: total facial height/bi-zygomatic breadth
  Reciprocal ponderal index: stature/$\sqrt[3]{\text{weight}}$
  Relative shoulder breadth: bi-acromial breadth/stature
  Relative sitting height: sitting height/stature.

TWINS

The various measurements were taken on a series of 21 female and 23 male mono-zygous pairs and 23 female and 14 male, like-sexed dizygous pairs. Except for 3 pairs who were undergraduates in the University of Michigan, the twins were from high schools and junior high schools in Ann Arbor, Ypsilanti, Dearborn, and Detroit. They ranged in age from 12 to 20 years, the median age being 16.

Twins were classified as dizygous if (1) they were discordant in either the ABO, MN, Rh, Kell, Duffy, or secretor reactions, the ABO and Rh types being based on the antisera A, absorbed A, and B and C, D, E, c, and e, respectively; if (2) the color or pattern of the iris of their eyes were conspicuously different; or if (3) their facial and head characters—including hair color—were markedly dissimilar. Other-wise they were classified as monozygous. A full discussion of the procedures employed in this study for diagnosing the zygosity of twins is given in another report (Sutton, Vandenberg, and Clark, in manuscript).

HERITABILITY

Heritability, designated by h^2, may for our present purposes be defined as the proportion of the variance within like-sexed dizygous twin pairs which is attributable to genetic factors. It may be estimated by

$$(1) \qquad\qquad h^2 = \frac{\sigma_D^2 - \sigma_M^2}{\sigma_D^2}$$

where σ_D^2 and σ_M^2 are the within-pair variances for dizygous and monozygous twins respectively. The significance of the difference between h^2 and zero is tested by the variance ratio $F = \frac{\sigma_D^2}{\sigma_M^2}$, there being 37 and 44 degrees of freedom for the dizygous and monozygous variances respectively. Estimates of σ_D^2, σ_M^2, and h^2 are given for each trait in Table I. In obtaining these estimates it was possible to combine the sexes and the various ages, since the within-pair variances could not be shown to differ in relation to either sex or age.

The variance within dizygous twins exceeds that within monozygous pairs for every character included in this report, the difference being significant at the 5% level for every trait except birth weight, bi-acromial breadth, relative shoulder breadth, waist circumference, and cephalic index. The fact that birth weight was not found to be significantly heritable is in accord with the results of other studies, such

as those of Dahlberg (1926) and Taniguchi (1955). The low heritability of waist circumference reflects the influence on this character of such environmental factors as diet and exercise. The values of h^2 for weight, stature, sitting height, head length, and head width are comparable with those reported by Newman, Freeman, and Holzinger (1937). For cephalic index, however, these authors obtained $h^2 = .75$, a result appreciably higher than our value of .38. The work of von Verschuer (1927) is not directly comparable with that reported here, since his analyses did not involve variances; but the values of h^2 given in Table I are consistent with his computations.

DISCUSSION

The estimation of heritability from a comparison of identical and fraternal twins involves the assumption that the environments of the two members of a set of monozygous twins are, on the average, neither more nor less different from one another than are the environments of the two members of a pair of dizygous twins of like sex. This assumption has been discussed by Price (1950). There is some evidence that the postnatal environments of monozygous twins are more similar than are those of dizygous twins. But because of the possibility of inbalance in the mutual circulation of monochorial monozygous embryos, and of other related phenomena, it is probable that the prenatal environments of monozygous twins are less alike than are those of dizygous twins. Assuming, however, the validity of the premise, heritability may be estimated by comparing the variance within pairs of dizygous twins, σ_D^2, with that within monozygous pairs, σ_M^2. The variance σ_D^2 contains a genetic, an environmental, and an error component, all of which are assumed to be additive, whereas σ_M^2 contains the environmental and error components only. The proportion of the total variance within like-sexed dizygous twins which may be attributed to genetic factors is therefore given by formula (1), as was shown by Holzinger (1929). Holzinger's expression,

$$(2) \qquad h^2 = \frac{r_M - r_D}{1 - r_D}$$

is equivalent to (1) if

$$(3) \qquad r_M = 1 - \frac{\sigma_M^2}{V}$$

and

$$(4) \qquad r_D = 1 - \frac{\sigma_D^2}{V},$$

where r_M and r_D are the intraclass correlations for monozygous and dizygous twins, respectively, and V is the total variance for all twins, both monozygous and dizygous. But if

$$(5) \qquad r_M = 1 - \frac{\sigma_M^2}{V_M}$$

and

$$(6) \qquad r_D = 1 - \frac{\sigma_D^2}{V_D},$$

where the variances V_M and V_D are computed separately for monozygous and dizygous twins respectively, then formula (2) is equivalent to

$$(7) \qquad h^2 = \frac{V_M \sigma_D^2 - V_D \sigma_M^2}{V_M \sigma_D^2}.$$

Since formula (7) is sensitive to sex, age and other between pair differences in the composition of the monozygous and dizygous samples, whereas (1) is insensitive to all such differences as do not affect the variances within pairs, we have employed (1) rather than (7) in our estimates of h^2.

It should be observed that the nongenetic component of the variation within dizygous twins, assumed to be estimated by σ_M^2, cannot be exactly equated with the environmental component since it also contains a component due to errors in measurement. For most of the anthropometric traits these errors are small, so that $1—h^2$ approximates the proportion of the variance attributable to environmental factors.

The statistic h^2 is an estimate, not of the extent to which a trait is genetically determined, but of the proportion of the variation in the trait which is genetically determined. If all of the genetic factors responsible for a character are identical in every individual in some population, the genetic component of the variance will be zero in that population—even if the genetic factors almost completely determine the character. Furthermore, h^2 is applicable only to the population from which it is derived. It is quite possible for a character that is heritable in one population not to be heritable in another, or for a trait that is not heritable among individuals at one age to be highly so among the same individuals at a later age.

Heritability, as measured by h^2, is nevertheless of considerable evolutionary interest, for it is an index of the susceptibility of a character to genetic change. That a character may be heritable at one age and not at another is a corollary of the fact that evolution may take place in one stage of the life cycle without affecting other stages. The possibility of differences in the heritability of a given character between populations is related to the fact that not all populations are equally sensitive to evolutionary change. A high value of h^2 does not necessarily indicate that a trait is undergoing rapid evolution, but the greater the value of h^2 for any character the greater may be the evolutionary effect of differential fertility with respect to that character.

The extent to which variation in anthropometric characters affects reproduction is unknown. The population sampled by this study, however, exhibits a considerable degree of genetically determined variability in these features. Should any of these anthropometric characters be correlated with fertility to an appreciable extent, evolutionary change in the characters concerned would be expected to occur.

SUMMARY

The genetic fraction, h^2, of the variance within pairs of like-sexed dizygous twins was estimated for a number of anthropometric characters. The greater part of the

variance of most of these traits was found to be genetically determined. If such characters were correlated with fertility they might be expected to undergo evolutionary change.

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