

*ESTIMATION OF THE LIMITS OF HERITABILITY OF TRAITS  
BY COMPARISON OF MONOZYGOTIC AND DIZYGOTIC TWINS*

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This paper has three aims: (1) to present a new formula for extracting heritability estimates from twin data; (2) to show the results of the application of the formula to data from past studies of the heritability of intelligence, scholastic achievement, personality traits, and physical characteristics; and (3) to urge that heritability estimates be obtained in all large-scale educational testing programs, in the standardization of intelligence, aptitude, and educational achievement tests, and in the Selective Service and Armed Forces qualification tests.

*Previous Estimates of Heritability.*—Although the twin method in itself does not provide sufficient information for testing detailed genetic models, it provides both the most efficient and the least ambiguous basis for an over-all estimate of heritability of quantitative traits.<sup>1</sup> Heritability ( $h^2$ ) is defined here as the proportion of phenotypic variance attributable to genotypic variance, i.e.,  $h^2 = \sigma_G^2/\sigma_P^2$ . The comparison of monozygotic (MZ) twins reared together and dizygotic (DZ) twins reared together is much more feasible and has been a much more common practice than the study of MZ twins reared apart. MZ twins reared apart are rare and difficult to find.<sup>2, 3</sup> Estimating heritability from MZ twins reared apart has the one advantage that it presents little theoretical difficulty, provided one can assume zero correlation between the relevant environmental effects acting on the separated twins, in which case  $h^2 = r_{MZ}$ , the intraclass correlation between MZ twins.

The prevailing method of estimating heritability from MZ and DZ twins has been by means of the  $H$  index devised by Holzinger.<sup>14</sup> That Holzinger's  $H$  index is not a satisfactory estimate of  $h^2$  is now generally recognized in behavior genetics, but the precise nature of the inadequacy of the  $H$  index and the problem of estimating  $h^2$  from MZ and DZ twin data have remained conceptually obscure.<sup>1, 4-6</sup> Nichols<sup>7</sup> proposed an improvement on the  $H$  index, called the  $HR$  index, but it, too, is unsatisfactory as an index of  $h^2$ . One serious criticism of  $H$  and  $HR$  is that one is not a monotonic function of the other, and neither is a monotonic function of  $h^2$ . Vandenberg<sup>1</sup> has proposed using  $F$  (the variance ratio) as a test of the significance of  $\sigma_{w_{DZ}}^2/\sigma_{w_{MZ}}^2$  (DZ within-pair variance/MZ within-pair variance), but this is as faulty as an index of heritability as the  $H$  index itself, since  $F$  is a linear function of  $H$ .<sup>8</sup> Determining the variance ratio  $F$ , however, is an essential step prior to computing  $h^2$ ; if  $F$  is not statistically significant,  $h^2$  cannot be presumed to differ significantly from zero.<sup>9, 10</sup>

*A New Formula for  $h^2$ .*—The rationale of the new formula for  $h^2$  based on the comparison of MZ and DZ twins is developed in the following 13 points. (In all cases, the correlations are corrected for unreliability. Also, if  $h^2$  is to be generalized to a population, it should be established that the total variances for either halves of the MZ and DZ pairs do not differ significantly from an estimate of the population variance.)

(1) Total true-score phenotypic variance (i.e., total variance – error variance):

$$\sigma_P^2 = \sigma_G^2 + \sigma_E^2 + \sigma_e^2, \quad (1)$$

where  $\sigma_P^2$  = phenotypic variance,  $\sigma_G^2$  = hereditary (genotypic) variance,  $\sigma_E^2$  = systematic environmental variance (between families),  $\sigma_e^2$  = unsystematic or random environmental variance (within families).

(2) Dividing equation (1) by  $\sigma_P^2$ :

$$1.00 = h^2 + E^2 + e^2,$$

where  $h^2 = \sigma_G^2/\sigma_P^2$  = heritability (the proportion of total variance due to heredity).

$E^2 = \sigma_E^2/\sigma_P^2$  = systematic environmental effects (proportion of total variance due to environmental differences between families (or conversely, environmental variance common to members of the same family).

$e^2 = \sigma_e^2/\sigma_P^2$  = unsystematic or random environmental effects (proportion of within family environmental variance).

(3) Holzinger's  $H$  index: 
$$H = \frac{r_{MZ} - r_{DZ}}{1 - r_{DZ}}.$$

(4) Nichols'  $HR$  index: 
$$HR = \frac{2(r_{MZ} - r_{DZ})}{r_{MZ}}.$$

(5)  $H$ ,  $HR$ , and  $h^2$  are not monotonic functions of one another. For example:

$r_{MZ}$	$r_{DZ}$	$H$	$HR$	$h^2$
1.00	0.50	1.00	1.00	1.00
0.40	0.20	0.25	1.00	0.40
0.90	0.80	0.50	0.22	0.20
1.00	0.99	1.00	0.02	0.02

(6) Correlation ( $r$ ) between sets of individuals,  $A$  and  $B$ , on a given trait:

$$r_{AB} = \rho_{GAB}h^2 + \rho_{EAB}E^2,$$

where  $\rho_{GAB}$  = genetic correlation between  $A$  and  $B$ .<sup>27</sup>

$\rho_{EAB}$  = correlation between relevant effects in environments of  $A$  and  $B$  (i.e., degree of environmental similarity).

(7) Generalized formula for  $h^2$  based on comparison of two groups of paired individuals ( $AB$  and  $CD$ ) such that  $\rho_{GAB} > \rho_{GCD}$ :

$$h^2 = \frac{r_{AB} - r_{CD} - E^2(\rho_{EAB} - \rho_{ECD})}{\rho_{GAB} - \rho_{GCD}}.$$

(8) Correlations between MZ twins reared together (MZT) and reared apart (MZA), with assumption that for MZT,  $\rho_E = 1$  and for MZA,  $\rho_E = 0$ . For both  $\rho_G = 1$ . (a)  $r_{MZT} = (1)h^2 + (1)E^2$ . (b)  $r_{MZA} = (1)h^2 + (0)E^2 = h^2$ .

(9) Correlation between DZ twins reared together:

$$r_{DZT} = \rho_\infty h^2 + (1)E^2,$$

where  $\rho_\infty$  = the genetic correlation between offspring (siblings).

(10) Estimation of  $h^2$  from comparison of MZ and DZ twins, with assumption that  $\rho_{EMZ} = \rho_{EDZ}$ . (a)  $r_{MZ} - r_{DZ} = (h^2 + E^2) - (\rho_\infty h^2 + E^2)$ . (b)  $h^2 = \frac{r_{MZ} - r_{DZ}}{1 - \rho_\infty}$ .

(11) Proportion of total variance due to systematic (between families) environmental differences:

$$E^2 = \frac{r_{DZ} - \rho_\infty r_{MZ}}{1 - \rho_\infty}.$$

(12) Proportion of total variance due to unsystematic (within families) environmental variance:

$$e^2 = 1 - h^2 - E^2 = 1 - r_{MZ}.$$

(13)  $\rho_{\infty}$  (the genetic correlation between siblings or DZ twins) derived from the genetic correlation between noninbred parents ( $\rho_{PP}$ ):<sup>11</sup>

$$\rho_{\infty} = \frac{1}{1 + 1/2\rho_{PP}} \cdot 1/2(1 + \rho_{PP}) = \frac{1 + \rho_{PP}}{2 + \rho_{PP}}$$

In terms of the traditional variance components model, the proposed formula yields a true estimate of  $h^2$  within the limits of sampling error, although it should be pointed out that this estimate of  $h^2$  also contains any variance attributable to the interaction of genotype and environment. However, the formula apparently yields the maximum amount of information concerning variance components that can be obtained from  $r_{MZ}$  and  $r_{DZ}$ . Furthermore, the new formula for  $h^2$  has the advantage of taking account of the genetic effects of assortative mating. The parameter  $\rho_{\infty}$  (genetic correlation between siblings) may be estimated for a given trait from theoretical or empirical considerations or both.<sup>27</sup> Taking account of  $\rho_{\infty}$ , the genetic correlation between siblings, permits greater precision in estimating  $h^2$  when there is some basis for determining the degree of assortative mating for the trait in question. In lieu of a precise estimate of assortative mating, one can obtain the extreme limits of  $h^2$  for a given set of data from some consideration of the reasonable bounds of assortative mating. For most traits, especially those in the abilities domain, the extreme limits would be  $\rho_{\infty} = 0.50$  (for siblings resulting from random mating) to  $\rho_{\infty} = 0.66$  (for siblings resulting, theoretically of course, from a self-mated mother). For some traits in which there might be negative assortative mating,  $\rho_{\infty}$  could take values less than 0.50. Negative assortative mating may occur for traits in the personality domain, where certain traits may be complementary in marital couples and thus negatively correlated, such as dominance-submissiveness.

*Results.*—Heritability estimates based on the various formulas are shown in Table 1. The first part of the table shows results from a number of studies,<sup>3, 7, 12-18</sup> using a variety of intelligence tests in different populations. The most extreme limits of  $h^2$  to be found in this table summarizing all the major twin studies using intelligence tests range from 0.42 (Swedish Military Induction Test) to 0.93 (Otis IQ test).<sup>19</sup> In considering this wide range of values, it should be kept in mind that heritability estimates are specific both to the population from which the twin samples are drawn and to the particular test used for measuring intelligence.

The most representative estimates are those based on the data summarized by Erlenmeyer-Kimling and Jarvick,<sup>16</sup> which represent the median values of all the twin studies reported in the literature up to 1963. We see that for these data the extreme lower and upper limits of  $h^2$  (going from random-mating to self-mating) are 0.72 and 0.90. Since there is known to be assortative mating for intelligence, the best estimates of  $h^2$  would be obtained from values of  $\rho_{\infty}$  (sibling genetic correlation) close to 0.55, resulting from a genetic correlation of 0.25 between parents. This yields  $h^2 = 0.80$ ,  $E^2 = 0.12$ , and  $e^2 = 0.08$ . Thus, according to these data—the average of all the major twin studies—four times as much of the variance in measured intelligence is attributable to heredity as to environment.

This statement can be expressed, also, in terms of the average difference in IQ between persons paired at random from the population.<sup>20</sup> Given an intelligence test like the Stanford-Binet, with a standard deviation of 16 IQ points in the white population of the United States, the average difference among such persons would be 18 IQ points. If everyone inherited the same genotype for intelligence (i.e.,  $h^2 = 0$ ), but all nongenetic environmental variance (i.e.,  $E^2 + e^2$ ) remained as is, people would differ, on the average, by 8 IQ points. On the other hand, if hereditary variance remained as is, but there were no environmental variation between families (i.e.,  $E^2 = 0$ ), the average difference among people would be 17 IQ points. If *all*

TABLE 1  
SUMMARY OF TWIN CORRELATIONS AND HERITABILITY ESTIMATES FOR INTELLIGENCE, SCHOLASTIC PERFORMANCE, AND PHYSICAL CHARACTERISTICS

Test or measures	Correlations <sup>a, b</sup>		F <sup>c</sup>	H	HR	Heritability Estimates <sup>d</sup>			e <sup>2</sup>							
	MZ Twin r	DZ Twin N				h <sup>2</sup> <sub>∞</sub> = 0.50 E <sup>2</sup>	h <sup>2</sup> <sub>∞</sub> = 0.55 E <sup>2</sup>	h <sup>2</sup> <sub>∞</sub> = 0.60 E <sup>2</sup>		h <sup>2</sup> <sub>∞</sub> = 0.68 E <sup>2</sup>						
Stanford-Binet IQ <sup>13</sup>	97	83	56	172	14.28	93	85	82	15	91	06	(102)	(-06)	(120)	(-24)	03
S-B IQ, adjusted scores <sup>13</sup>	98	83	58	172	20.00	95	83	80	15	89	06	(100)	(-05)	(118)	(-23)	05
Binet IQ <sup>14</sup>	93	50	66	52	4.61	78	57	53	40	59	34	66	27	78	15	07
Binet IQ <sup>15</sup>	96	50	67	50	7.75	87	59	57	39	63	33	71	25	84	12	04
Otis IQ <sup>15</sup>	97	50	65	50	11.24	91	65	63	34	70	27	79	18	93	04	03
Various intelligence measures <sup>16</sup>	92	14 <sup>d</sup>	56	11 <sup>e</sup>	5.26	81	78	72	20	80	12	90	02	(105)	(-14)	08
Dominos Test and Mill Hill Vocabulary <sup>3</sup>	80	44	54	44	2.31	57	66	53	27	58	22	66	14	77	03	20
Primary Mental Abilities Composite <sup>26</sup>	79	26	41	26	2.80	64	96	76	03	(84)	(-05)	(95)	(-16)	(111)	(-32)	21
Swedish Military Induction Test <sup>17</sup>	95	215	74	42	5.05	80	44	42	53	47	48	53	42	62	33	05
National Merit Scholarship Qualification Test <sup>7</sup>	92	687	66	482	4.02	75	55	51	41	56	35	63	28	74	17	08
Educational age <sup>15</sup>	94	50	73	50	4.38	77	44	41	53	46	46	52	42	61	33	06
General scholastic achievement <sup>13</sup>	95	83	87	172	2.42	59	16	15	80	16	78	19	76	22	73	05
Reading and spelling <sup>13</sup>	99	83	97	172	3.10	68	04	04	95	05	94	05	94	06	93	01
Reading <sup>18</sup>	94	134	65	180	5.49	82	61	57	37	63	31	71	23	84	10	06
Arithmetic <sup>13</sup>	91	83	79	172	2.23	55	26	23	67	25	66	29	62	34	57	09
Arithmetic <sup>18</sup>	92	134	55	181	5.38	81	80	74	18	82	10	(92)	(-00)	(108)	(-17)	08
Standing height <sup>13</sup>	96	83	47	172	13.16	92	102	(98)	(-02)	(109)	(-13)	(123)	(-27)	(144)	(-48)	04
Standing height <sup>15</sup>	93	50	64	50	5.21	81	62	57	36	64	30	72	21	84	09	07
Weight <sup>13</sup>	93	83	59	172	5.85	83	73	68	25	76	18	85	08	(100)	(-07)	07
Weight <sup>15</sup>	92	50	63	50	4.44	78	62	57	35	64	28	72	20	84	08	08
Head length <sup>13</sup>	96	83	50	172	12.50	92	96	92	04	(102)	(-06)	(115)	(-19)	(135)	(-39)	04
Head length <sup>15</sup>	91	50	58	50	4.63	78	72	65	26	73	18	82	09	(961)	(-05)	09
Head breadth <sup>13</sup>	98	83	54	172	22.73	96	90	88	10	98	00	(110)	(-12)	(129)	(-31)	02
Head breadth <sup>15</sup>	89	50	55	50	4.06	75	77	69	20	76	13	86	03	(101)	(-12)	11
Eye color <sup>13</sup>	100	50	52	50	∞	100	96	96	04	(107)	(-07)	(120)	(-20)	(141)	(-41)	00

<sup>a</sup> Correlations of mental and scholastic tests corrected for attenuation; correlations for physical measurements not corrected. <sup>b</sup> Decimals omitted. <sup>c</sup> F, the variance ratio of DZ within-pair variance/MZ within-pair variance. All values of F in this column are significant beyond the 0.01 level. <sup>d</sup> Median of 14 independent studies. <sup>e</sup> Median of 11 independent studies.

nongenetic sources of individual differences were removed (i.e.,  $E^2 + e^2 = 0$ ), the average intellectual difference among people would be 16 IQ points. (Error in measurement has been subtracted from all these figures.) These results decidedly contradict the popular notion that the environment is of predominant importance as a cause of individual differences in measured intelligence in our present society. The results show, furthermore, that current IQ tests certainly do reflect innate intellectual potential (to a degree indicated by  $h^2$ ), and that biological inheritance is far more important than the social-psychological environment in determining differences in IQ's. This is not to say, however, that as yet undiscovered biological, chemical, or psychological forms of intervention in the genetic or developmental processes could not diminish the relative importance of heredity as a determinant of intellectual differences.

*Scholastic achievement:* The middle section of Table 1 summarizes studies based on tests of scholastic achievement. In general, individual differences in scholastic performance are determined less than half as much by heredity than are individual differences in intelligence.<sup>21</sup> The largest source of individual differences in school achievement is the environmental differences *between* families. Variance in achievement due to differential environmental effects *within* families is extremely small.

The fact that school achievement is highly susceptible to environmental influences, while intelligence apparently is not, suggests important implications for education that have not yet been explored.

*Physical characteristics:* The third section of Table 1 is interesting for compara-

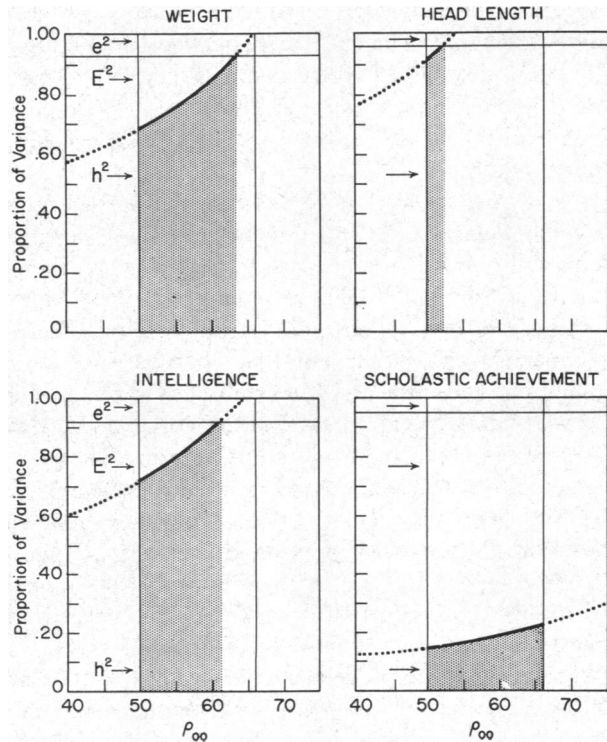


FIG. 1.—Graphic representation of the limits of  $h^2$ ,  $E^2$ , and  $e^2$ . The values are computed between the range of  $\rho_{oo} = 0.50$  (sibling genetic correlation under random-mating) and  $\rho_{oo} = 0.66$  (sibling genetic correlation under self-mating). The shaded area shows the actual possible values for a particular study yielding specific values for  $r_{MZ}$  and  $r_{DZ}$ . The dotted portion of each curve represents a range of values beyond "reasonable" limits for the traits in question. (Data: weight,<sup>12</sup> head length,<sup>12</sup> intelligence,<sup>16</sup> scholastic achievement.)<sup>13</sup>

TABLE  
HERITABILITY OF

Personality scales	Correlations†		H	HR
	MZ	DZ		
MMPI‡				
Social introversion	45	12	37	147
Depression	44	14	35	136
Psychoasthenia	41	11	34	146
Psychopathic deviate	48	27	28	88
Schizophrenia	44	24	27	91
Paranoia	27	08	21	141
Hysteria	37	23	19	76
Hypochondriasis	41	28	17	63
Hypomania	32	18	17	88
Masculinity-femininity	41	35	09	29
CPI§				
Self-control	56	27	40	105
Rigidity	47	13	39	147
Dominance	58	13	52	155
Responsibility	57	29	39	98
Intellectual efficiency	59	27	43	107

\* Decimals omitted.

† Not corrected for attenuation. Decimals omitted.

tive purposes, showing results for highly heritable physical characteristics. (Since for these there is probably little assortative mating, the most plausible values of  $\rho_{\infty}$  would lie between 0.50 and 0.55.) It can be seen that over-all the heritability of intelligence is closer to that for physical characteristics such as height, weight, and head length than to scholastic achievement.

Figure 1 presents these results graphically. The shaded area is the range of possible values of  $h^2$  when  $\rho_{\infty}$  varies between 0.50 and 0.66. This form of graphic presentation may be useful for comparing various tests given to the same population or for comparing various subgroups in the population on a particular test. For statistical purposes, confidence bands<sup>22</sup> can be placed around the lines separating  $h^2$ ,  $E^2$ , and  $e^2$ .

*Personality traits:* Table 2 summarizes the heritability estimates for a number of personality scales.<sup>23, 24</sup> For most of these personality traits "impossible" values of  $h^2$  and  $E^2$  result when  $\rho_{PP} > 0$ , that is, when there is positive assortative mating. It may well be that this genetic additive model is grossly inappropriate for dealing with heritability of personality traits. The personality measures differ most conspicuously from intelligence, scholastic achievement, and physical traits in yielding large values of  $e^2$  (within family environmental variance) as compared with  $E^2$  (between family of environmental variance). Also,  $h^2$  shows much greater sex differences for personality traits than for abilities. In terms of the present formulation of  $h^2$ , there are obviously serious difficulties in making sense out of the twin data on personality scales. Precisely where the trouble lies is not understood, but the present formulation at least highlights the problem.

*Further applications of  $h^2$ :* Finally, because the estimation of heritability provides important information concerning sources of variance in our tests, I would urge that provision for assessing heritability become a routine part of large-scale educational testing programs, test standardization, and ability testing in the Armed Forces. Modern data-processing techniques now make this entirely feasible. The practice would require that testees carefully identify all their blood relations who

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## PERSONALITY TRAITS

Heritability Estimates*								
$\rho_{PP} = -1.00$ $\rho_{\infty} = 0.00$		$\rho_{PP} = -0.66$ $\rho_{\infty} = 0.25$		$\rho_{PP} = 0.00$ $\rho_{\infty} = 0.50$		$\rho_{PP} = 1.00$ $\rho_{\infty} = 0.66$		
$h^2$	$E^2$	$h^2$	$E^2$	$h^2$	$E^2$	$h^2$	$E^2$	$e^2$
33	12	44	01	(66)	(-21)	(99)	(-54)	55
30	14	40	04	(60)	(-16)	(90)	(-46)	56
30	11	40	01	(60)	(-19)	(90)	(-49)	59
21	27	28	20	42	06	(63)	(-15)	52
20	24	27	17	40	04	(60)	(-16)	56
19	08	25	02	(38)	(-11)	(57)	(-30)	73
14	23	19	18	28	09	(32)	(-05)	63
13	28	17	24	26	15	39	02	59
14	18	19	13	28	04	(42)	(-10)	68
06	35	08	33	12	29	18	23	59
29	27	38	18	(58)	02	(87)	(-13)	44
34	13	45	02	(68)	(-21)	(102)	(-55)	53
45	13	(60)	(-02)	(90)	(-32)	(135)	(-77)	42
28	29	37	20	56	01	(84)	(-27)	43
32	27	43	16	(64)	(-05)	(96)	(-37)	41

† Minnesota Multiphasic Personality Inventory data ( $N = 120$  MZ, 132 DZ pairs) from Vandenberg<sup>2†</sup> (1966).

‡ California Personality Inventory data (males only,  $N = 207$  MZ, 120 DZ pairs) from Nichols<sup>2‡</sup> (1966).

are likely to be in the tested population: parents, siblings, half siblings, cousins, and especially twins. The zygosity of twins can now be determined with better than 90 per cent accuracy by means of a brief questionnaire.<sup>25</sup> We know that tests of ability differ widely in the degree to which they reflect innate factors on the one hand, or social, cultural, and educational influences on the other. Heritability estimates thus can provide important information concerning major classes of variables determining individual differences on a given test.

One criterion of a "culture-free" or "culture-fair" test is the degree to which it yields high estimates of  $h^2$  in a population in which there is actually a wide range of environmental variation. Do culturally or economically disadvantaged minority groups within our population show lower heritability than more advantaged groups in test scores used for job placement, for educational selection, and for determining qualification for the Armed Services? Although  $h^2$  has no necessary connection with a test's validity for predicting some criterion, such as suitability for the Armed Forces or success in college,  $h^2$  should be of great interest to educators, since  $1 - h^2$  is an indication of the proportion of variance in abilities we potentially can influence by educational and social-psychological means. Large-scale testing programs should try to account for as many of the major sources of variance in test scores as possible. Three of these sources are defined by  $h^2$ ,  $E^2$ , and  $e^2$ .

\* On leave (1966-1967) from the University of California, Berkeley.

<sup>1</sup> Vandenberg, S. G., *Psychol. Bull.*, **66**, 327 (1966).

<sup>2</sup> Burt, C., *Brit. J. Psychol.*, **57**, 137 (1966).

<sup>3</sup> Shields, J., *Monozygotic Twins Brought Up Apart and Brought Up Together* (London: Oxford University Press, 1962).

<sup>4</sup> Fuller, J. L., and W. R. Thompson, *Behavior Genetics* (New York: Wiley, 1960), pp. 113-114.

<sup>5</sup> Gottesman, I. I., in *Handbook of Mental Deficiency*, ed. N. Ellis (New York: McGraw-Hill, 1963), p. 266.

<sup>6</sup> Neel, J. V., and W. J. Schull, *Human Heredity* (Chicago: University of Chicago Press, 1954), p. 275.

<sup>7</sup> Nichols, R. C., in *Methods and Goals in Human Behavior Genetics*, ed. S. G. Vandenberg (New York: Academic Press, 1965).

$$^8 F = 1/(1 - H).$$

<sup>9</sup> The validity of  $F$  as a test of statistical significance in this case requires the assumption that the distributions corresponding to  $\sigma w_{DZ}^2$  and  $\sigma w_{MZ}^2$  do not differ significantly in kurtosis.

<sup>10</sup>  $h^2$  cannot be computed in those rare cases where  $r_{MZ} < r_{DZ}$ , since this would yield negative heritability. If  $r_{MZ}$  is significantly less than  $r_{DZ}$ , one reasonable interpretation is that for the particular trait in question MZ twins take on complementary (rather than similar) roles to a greater degree than do DZ twins.

<sup>11</sup> Li, C. C., *Population Genetics* (Chicago: University of Chicago Press, 1955), ch. 13.

<sup>12</sup> Burt, C., *Brit. J. Educ. Psychol.*, **25**, 158 (1955).

<sup>13</sup> Burt, C., *Am. Psychol.*, **13**, 1 (1958).

<sup>14</sup> Holzinger, K. J., *J. Educ. Psychol.*, **20**, 241 (1929).

<sup>15</sup> Newman, H. H., F. N. Freeman, and K. J. Holzinger, *Twins: A Study of Heredity and Environment* (Chicago: University of Chicago Press, 1937).

<sup>16</sup> Erlenmeyer-Kimling, L., and L. F. Jarvik, *Science*, **142**, 1477 (1963).

<sup>17</sup> Husén, T., *Psychological Twin Research* (Stockholm: Almqvist & Wiksell, 1959), vol. 1.

<sup>18</sup> Husén, T., *Scand. J. Psychol.*, **1**, 125 (1960).

<sup>19</sup> Note that for some values of  $\rho_\infty$ ,  $h^2$  exceeds 1.00 and  $E^2$  becomes a negative value. These "impossible" values (enclosed in parentheses in Table 1) set the upper limit of the estimate of  $\rho_\infty$ .

<sup>20</sup> Assuming a normal distribution in the population, the mean absolute difference between all possible pairs of scores in the distribution is given by Gini's formula:  $|\bar{x}| = 2\sigma/\sqrt{\pi}$  (Kendall, M. G., *The Advanced Theory of Statistics* (New York: Hafner, 1960), 3d ed., vol. 1, pp. 241-242). The mean absolute difference when the proportion of variance attributable to heredity,  $h^2$ , is removed =  $2\sqrt{\sigma^2(1 - h^2)}/\sqrt{\pi}$ .

<sup>21</sup> Rank in high school graduating class has values of  $h^2$  ranging from 0.16 to 0.24 for males (for  $\rho_\infty = 0.50-0.66$ ) and 0.28 to 0.42 for females; corresponding values of  $E^2$  for males are 0.67 to 0.59 and for females 0.62 to 0.48.<sup>26</sup>

<sup>22</sup> The confidence limits for  $h^2$  are determined by using the standard errors of  $r_{MZ}$  and  $r_D$  ( $SE_r = (1 - r^2)/\sqrt{N - 1}$ ). The upper and lower limits of  $r_{MZ}$  and  $r_{DZ}$  are set by  $r \pm (x) SE_r$ , where  $x$  is the number of  $SE_r$ 's for a given level of confidence,  $P$ . From these upper and lower limiting values of both  $r_{MZ}$  and  $r_{DZ}$ , the upper and lower limits of  $h^2$  are calculated. The probability that the true value of  $h^2$  lies outside these limits is  $P^2$ . Essentially the same procedure is used to obtain confidence limits for  $E^2$  and  $e^2$ .

<sup>23</sup> Vandenberg, S. G., *Louisville Twin Study, Research Rep. No. 19*, University of Louisville School of Medicine, Louisville, Kentucky (1966).

<sup>24</sup> Nichols, R. C., *National Merit Scholarship Corporation Research Reports*, **2**, No. 8 (1966).

<sup>25</sup> Nichols, R. C., and W. C. Bilbro, Jr., *Acta Genet.*, **16**, 265 (1966).

<sup>26</sup> Blewett, D. B., *J. Mental Sci.*, **100**, 922 (1954).

<sup>27</sup> The parameter  $\rho$  includes more than what geneticists generally refer to as the genetic correlation;  $\rho$  is actually a weighted average of the proportions of additive, dominance, and epistatic sources of genetic variance. Therefore,  $\rho$  is a complex quantity whose value is close to  $1/2$  but is not known precisely. Because of dominance and epistasis,  $\rho$  may be less than  $1/2$  under random mating, and if dominance and epistasis are large relative to the additive genic effect,  $\rho$  could be less than  $1/2$  even under assortative mating. The total genetic variance,  $h^2$ , cannot be precisely analyzed into additive, dominance, and interactive effects on the basis of twin data alone.