GENETIC AND EXTRAGENETIC VARIANCE IN MOTOR PERFORMANCE

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A simple additive model of genes plus environment, based on intrapair similarities observed in 35 MZ and 35 like-sexed DZ twin pairs, was used to estimate the relative contribution of genetically controlled phenotypic variance in psychomotor individuality. Subjects practiced 50 trials on a pursuit rotor apparatus under a 20-sec/20-sec, work-rest schedule with a 30 min rest pause allowed between trials 30 and 31. Analyses of the data disclosed that a greater proportion of genetic factors, as opposed to nongenetic factors, appears to account for existing individual differences in motor performance among individuals subject to similar environmental conditions. The strength of this genetic control, however, systematically diminished throughout the course of practice obeying a monotonic trend over trials.

INTRODUCTION

Studies pertaining to the heritability of anthropometric dimensions (Vandenberg 1962, Gedda et al. 1964, Mizuno 1965, Hirata 1966) and motor performance (McNemar 1933, Brody 1937) support the contention that the genetic influence to motor performance and successful athletic participation substantially outweigh the nongenetic influences. Scarr (1966), however, reported only moderate heritability coefficients for activity level and reaction time, whereas Williams and Hearfield (1973) found approximately equal genetic and extragenetic influences to individual differences in the performance of a ladder climb task.

This study, therefore, examined the extent to which the relative genetic potency accounted for interindividual variation throughout the course of practice on a motor task.

The rationale of heritability studies frequently involves a comparison of intrapair similarities between MZ and DZ twins. Since identical twins share their genetic identity, the phenotypic variance expressed in the performance of a motor task is due solely to environmental agents, whereas that in nonidentical twins is due to both genetic and extragenetic sources. Further, when MZ and DZ twin pairs are raised in comparable environments, a comparison of the degree of resemblance between the twin pairs provides a basis for evaluating the extent to which phenotypic variance is controlled by genetic predisposition.

The design employed in the study necessitated specific assumptions. First, the tenability of the assumption of similar environmental influences for MZ and DZ twins must be considered from both prenatal and postnatal environments. According to Robinson (1938), any irregularities in intrauterine position, blood supply to the embryo, and accidental differences in cytoplasmic make-up, may result in structural and biochemical differences between twins.

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Schoenfeldt (1969), however, has suggested these prenatal differences are not enduring but are progressively equalized under the influence of a genetic maturational pacemaker. Further, the assumption of similar postnatal environments for MZ and DZ twins does not imply invariant environments, but that it varied approximately in the same direction and to the same degree for all individuals in the study. Vandenberg (1966) has suggested that for psychological-motor functions and for cognitive abilities, one could envisage some division of labor or specialization occurring within a twin pair such that one twin develops more in one direction. This may occur in MZ as well as DZ twins and, even if it happens more in DZ twins, it may be attributable to a greater initial divergence resulting from hereditary differences. Also, if environmental influences within the family are in part responsible for greater differences in motor ability within DZ twin pairs than within MZ twin pairs, one might expect that the correlations between the differences of twins on a variety of tests would be quite high. Vandenberg (1966) pointed out, however, that this was not the case. Finally, Block (1968) has suggested that the findings regarding unequal intrauterine conditions and the effects of differential parental treatment of twins are equivocal and no definitive conclusions may be noted.

Heritability

The prevailing methods of estimating heritability (defined as the proportion of phenotypic variance attributable to genotypic variance) from twin data have been the *HR index* of Nichols (1965) and the *H index* devised by Holzinger (1929). Jensen (1967), however, offered a generalized formula for h^2 based on a comparison of related groups such that the theoretical resemblance between one group is greater than the theoretical resemblance of another group. Thus, in the present study, heritability estimates of motor performance over blocks of practice trials were derived on the basis of the following equation:

$$h^2 = \frac{r_{MZ} - r_{DZ} - E^2(\rho E_{MZ} - \rho E_{DZ})}{\rho G_{MZ} - \rho G_{DZ}} \quad (1)$$

where:

h^2 = heritability;
$r_{MZ(DZ)}$ = correlation coefficient between member pairs of twins;
E^2 = systematic environmental effects;
$\rho E_{MZ(DZ)}$ = correlation between relevant effects in the environments of the twins[1];
$\rho G_{MZ(DZ)}$ = theoretical genetic correlation between member pairs of twins.

Two types of correlation coefficients (age and sex of the subjects held constant) were used to derive comparative sets of heritability coefficients. First, the intraclass correlation (r_i) was used to estimate the genetic contribution to the total phenotypic variance of a particular variable as follows:

$$r_i = \frac{S^2B - S^2W}{S^2B + (n-1)\ S^2W} \quad (2)$$

where:

r_i = intraclass correlation coefficient;
S^2B = between-pairs variance;
S^2W = within-pairs variance;
n = number of twin pairs.

[1] The parameter ρ representing the genetic correlation between siblings is actually the weighted average of the proportions of additive, dominance, and epistatic sources of genetic variance. This parameter necessarily remains nebulous, since heritability cannot be precisely analyzed in terms of these components on the basis of twin data alone. However, it is unlikely there is any substantial degree of assortative mating for pursuit rotor ability. Thus, this parameter was assigned a value commensurate with random mating.

An additional estimate of heritability was obtained by calculating correlation coefficients (r_c) based on an estimate of the population[2] variance (S^2T) and the within-pair variance (McNemar 1962, Kerlinger 1967) of a particular twin group as follows:

$$r_c = 1 - (S^2W/S^2T) \tag{3}$$

where:

r_c = correlation coefficient;
S^2W = within-pair variance of a twin group;
S^2T = estimate of the population variance.

Thus, a simple additive model of genes plus environment was used to estimate the relative strength of the genetically controlled phenotypic variance over the course of practice on the motor task. Different statistical techniques to calculate twin-pair relationships were used in the model to provide a more stable and conservative estimate of heritability.

METHODS

Subjects

MZ twins (n = 35 pairs) and like-sexed DZ twins (n = 35 pairs), ranging in age from 11 to 18 years ($\bar{x}$ = 15.6 years), served as subjects in the study. The distribution of twin pairs is shown in Table 1. These subjects, unfamiliar with practice on the pursuit rotor apparatus, were classified as MZ or DZ on the basis of their responses to a prepared questionnaire and zygosity diagnosis procedure described by Nichols and Bilbro (1966). All subjects were also given a PTC taste test as an additional aid to the diagnosis of zygosity.

Table 1. *Distribution of twin pairs*

	Male pairs		Female pairs		Total	
	N	Mean age (in months)	N	Mean age (in months)	N	Mean age (in months)
MZ pairs	18	188.28	17	191.24	35	189.76
DZ pairs	21	185.38	14	185.21	35	185.30
Total	39	186.83	31	188.23	70	187.53

Apparatus

The Koerth-type pursuit apparatus (Ammons and Ammons 1970) used in the study had a 25.5 cm diameter turntable that revolved at a constant speed of 60 rpm. The target, a 2 cm metal contact disc imbedded flush with the turntable, described an orbit of 8.3 cm in radius. A hinged, metal-tipped stylus 26 cm in length was used to contact the target as it revolved. The stylus was hinged so that it was not possible to facilitate tracking of the target nor influence rotation of the turntable. Standard electric chronoscopes, calibrated in 0.01 sec, were connected to the rotor in order to record the duration of each trial and the amount of time on target per trial.

Experimental Procedure

The zygosity diagnosis questionnaire was given prior to actual practice on the motor task but the twins were not classified as MZ or DZ until the task had been completed. The individual twin subject was then shown the physical procedure of the task and allowed 50 practice trials under a 20 sec/20 sec work-rest schedule. Scores were recorded on electric chronoscopes as amount of time on target per 20 sec work interval. A 30 min rest was allowed between trials 30 and 31 in order to estimate the relative genetic strength over the rest interval.

[2] The variance of the total twin sample (n = 140 subjects) was used as an estimate of the population variance, since it is not influenced by the instability of the variance within each twin group.

RESULTS AND DISCUSSION

The performance scores of twins over the course of practice on the motor task were comparable to that of singletons. That is, learning occurred in an exponential fashion and to essentially the same magnitude and rate as singletons.

Due to the trial-by-trial score fluctuation and difficulty in locating a trend for heritability over the 50 trials, estimates of heritability were derived from successive blocks of trials. Prior to this calculation, however, it was necessary to determine the optimal number of trials required to provide a reliable estimate of performance per trial block. Thus, a successively increasing number of performance scores were pooled and the respective reliability coefficients were calculated (Winer 1971). It was found that satisfactory coefficients were obtained when the average of 5 trials was used as an estimate of performance per trial block. These data, presented in Table 2, show reliability coefficients ranging from 0.91 to 0.95 for both twin groups.

Table 2. *Reliability coefficients for successive blocks of five trial scores*

Trial blocks	MZ twins	DZ twins
1-5	0.935	0.949
6-10	0.921	0.908
11-15	0.937	0.918
16-20	0.921	0.920
21-25	0.934	0.929
26-30	0.939	0.931
31-35	0.933	0.912
36-40	0.932	0.939
41-45	0.936	0.927
46-50	0.947	0.937

The ratio of the DZ and MZ intrapair variance was used to test the significance of the difference between the two twin groups over trial blocks. This analysis determined whether or not further computation was necessary. If F is not shown to be statistically significant, h^2 cannot be presumed to differ significantly from zero and any inference thus drawn would have little meaning. The F ratios were calculated such that the variance within DZ twin

Table 3. *Ratio of intrapair variance for MZ and DZ twins over trial blocks*

Trial blocks	S^2_{DZ}	S^2_{MZ}	$F = S^2_{DZ}/S^2_{MZ}$
1-5	1.45	0.63	2.30
6-10	1.56	0.64	2.44
11-15	2.42	1.10	2.20
16-20	2.69	1.27	2.12
21-25	2.42	0.87	2.78
26-30	2.15	1.04	2.07
31-35	5.38	1.04	5.17
36-40	4.26	0.78	5.46
41-45	4.65	0.87	5.96
46-50	3.16	1.08	2.93

All F ratios significant at the 0.05 level.

pairs was expected to exceed that in MZ twins, since the variability for DZ twins is the result of both environmental and genetic factors. The results of this analysis are shown in Table 3 and show F ratios ranging from 2.07 to 5.96 over the 10 blocks of trials ($p<0.05$). As shown in Table 4, the MZ and DZ intraclass correlations provided the first set of heritability coefficients. Over all trial blocks, the MZ twin pair coefficients were greater than the corresponding coefficients for the DZ twin pairs. The heritability estimates showed relatively high values for performance initially in practice of the task and then a gradual decrease over trial blocks to the final prerest trial block. Heritability coefficients during postrest practice indicated a similar decreasing trend over trial blocks. The heritability coefficients ranged from 0.45 to 0.98 while the standard error of these estimates ranged from $\pm$ 0.06 to $\pm$ 0.10 over the 10 blocks of trials.

Table 4. *Intraclass correlation coefficients and heritability estimates over trial blocks*

Trial blocks	R_i(MZ)	R_i(DZ)	h^2	h^2(SE)
1-5	0.73	0.25	0.96	$\pm$0.06
6-10	0.84	0.46	0.77	$\pm$0.08
11-15	0.81	0.32	0.98	$\pm$0.09
16-20	0.80	0.50	0.61	$\pm$0.09
21-25	0.87	0.57	0.61	$\pm$0.08
26-30	0.85	0.63	0.45	$\pm$0.10
31-35	0.87	0.45	0.85	$\pm$0.06
36-40	0.90	0.56	0.67	$\pm$0.06
41-45	0.88	0.48	0.79	$\pm$0.06
46-50	0.85	0.56	0.58	$\pm$0.09

It should be noted that comparisons of the intraclass correlations for MZ and DZ twins is a minimal estimate of the genetic contribution to behavior in a population whose MZ and DZ cotwin environments are approximately equivalent (Scarr 1966). On the other hand, if the variance of the representative samples is dissimilar, the magnitude of the intraclass correlations can be a deceptive indicator of the actual magnitude of the twin differences (or similarities) relative to the population variance.

Computation of a parallel set of heritability estimates was obtained by comparing MZ and DZ twin correlation coefficients that were based on an estimate of the population variance and the intrapair variance of a particular twin group. These results are shown in Table 5.

Table 5. *Corrected correlation coefficients and heritability estimates over trial blocks*

Trial blocks	R_c(MZ)	R_c(DZ)	h^2	h^2(SE)
1-5	0.70	0.30	0.79	$\pm$0.08
6-10	0.81	0.54	0.55	$\pm$0.09
11-15	0.76	0.47	0.57	$\pm$0.09
16-20	0.78	0.53	0.49	$\pm$0.10
21-25	0.86	0.60	0.51	$\pm$0.08
26-30	0.84	0.66	0.35	$\pm$0.09
31-35	0.88	0.38	0.99	$\pm$0.05
36-40	0.91	0.50	0.82	$\pm$0.05
41-45	0.89	0.41	0.96	$\pm$0.05
46-50	0.85	0.55	0.59	$\pm$0.09

The heritability estimates based on these correlations also revealed a substantial, although somewhat less, genetic contribution to total phenotypic variance, as well as a similar decreasing trend over trial blocks. The heritability coefficients ranged from a low value of 0.35 prior to rest to a value of 0.99 in the first postrest trial block. The fact of a relatively greater genetic control than nongenetic control to individual differences in motor performance was reflected in the heritability estimates for the trial blocks. This finding is consistent with previous studies of motor tasks involving such skills as tapping speed (Eysenck and Prell 1951), pursuit rotor ability and card sorting (McNemar 1933, Vandenberg 1962), and manual manipulation (Brody 1937).

The means of the two sets of heritability coefficients were calculated in order to estimate the genetic strength over trial blocks. As well, the proportion of total variance due to environmental differences between families (E^2) was calculated. The theoretical genetic correlation between siblings ($P\infty$) was used in the equation as follows:

$$E^2 = \frac{r\ \mathrm{DZ} - P\infty\ (r\ \mathrm{MZ})}{1 - P\infty}$$

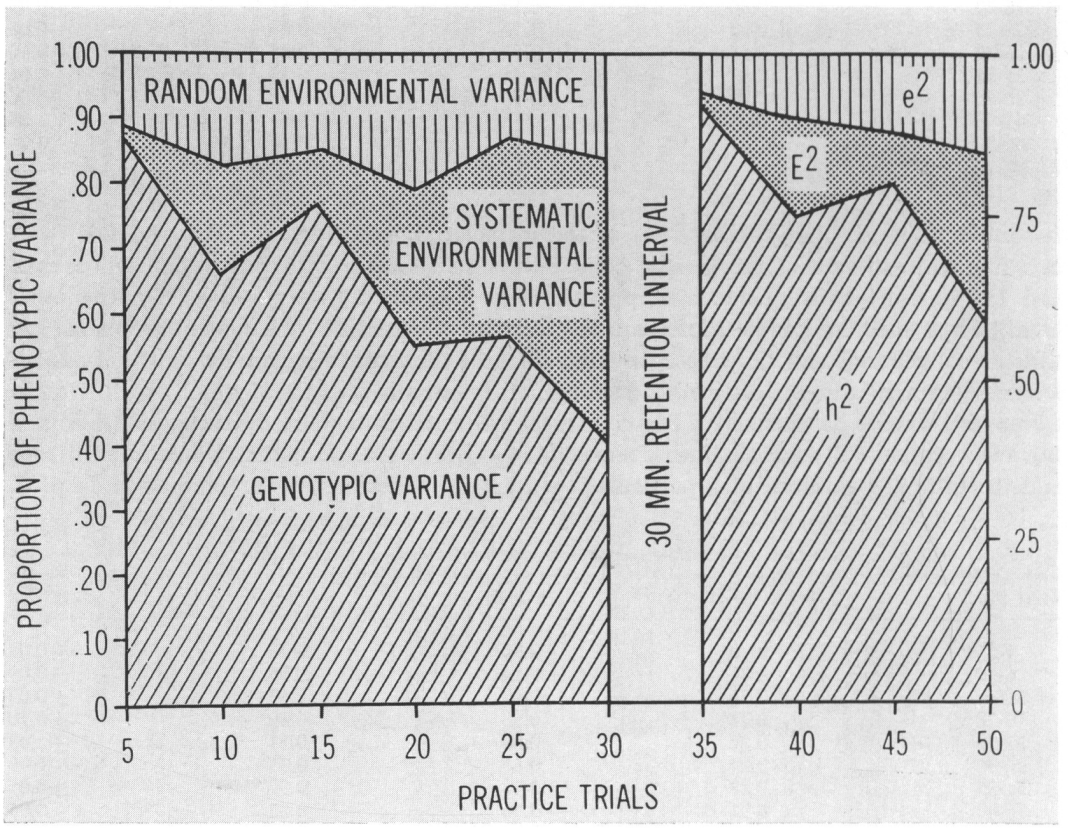

Figure. Proportion of total true-score phenotypic variance (σp^2) accounted for by heredity (h^2), between-families environmental variance (σE^2) and within-families environmental variance (σe^2).

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The within-families environmental variance (e^2) was then obtained by subtracting that proportion of variance due to E^2 and h^2 from unity (Jensen 1967). These results are shown in the Figure. Observation of this figure shows that high heritability by itself does not necessarily imply that a particular characteristic is immutable since the proportion of phenotypic variance accounted for by genetic predisposition is shown to decrease throughout practice. Conversely, the nongenetic contribution to individual differences increased over trial blocks, to the extent that at the final prerest trial block, individual differences in motor performance were determined less than half as much by heredity than by environmental differences. Observation of the postrest blocks of trials also shows a similar decrease in the ratio of genetic to phenotypic variance.

McNemar (1933) concluded that practice on the pursuit rotor task increased the resemblance of fraternal twins but had little effect on the degree of resemblance of identical twins. The obvious result of this differential increase in DZ resemblance would be to systematically decrease the heritability coefficients that are based on these correlations. As well, Noble (1969) has hypothesized that the ratio of heredity to environmental variance would be greater in the early stages of practice on a novel, culturally nonspecific task, but this ratio would undergo systematic changes with the amount of training and type of experience. Wilde (1970), in a reanalysis of data from pursuit rotor (McNemar 1933) and mechanical ability test (Brody 1937), concluded that heredity approaches zero with increasing practice on the tasks.

It was concluded that, initially in the practice of a motor task, a relatively greater proportion of genetic factors as opposed to extragenetic factors appears to account for existing individual differences in motor performance among individuals subject to similar environmental conditions. The strength of this genetic control, however, systematically diminishes throughout the course of practice obeying a monotonic trend over trials.

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RIASSUNTO

Varianza Genetica ed Extragenetica nell'Attività Motoria

Sulla base delle somiglianze intracoppia osservate in un campione di 35 coppie di gemelli MZ e 35 di gemelli DZ dello stesso sesso, è stata effettuata una valutazione del contributo genetico nella varianza fenotipica dell'individualità psicomotoria. L'analisi dei dati sperimentali ha dimostrato che i fattori genetici hanno una maggiore responsabilità di quelli non genetici nella determinazione delle differenze individuali nell'attività motoria a parità di condizioni ambientali. L'entità del controllo genetico si riduce, tuttavia, man mano che procede l'allenamento.

RÉSUMÉ

Variance Génétique et Extragénétique dans l'Activité Motrice

Une évaluation de la contribution génétique dans la variance phénotypique de l'individualité psychomotrice a été effectuée sur la base de l'étude des ressemblances intra-couple sur un échantillon de 35 couples de jumeaux MZ et 35 de jumeaux DZ du même sexe. L'analyse des données expérimentales a démontré que les facteurs génétiques sont plus responsables des facteurs non-génétiques dans la détermination des différences individuelles dans l'acitvité motrice. Le rôle des facteurs génétiques se réduit, d'ailleurs, au fur et à mesure que l'activité augmente.

ZUSAMMENFASSUNG

Genetische und extragenetische Varianz der Motorik

Aufgrund der Ähnlichkeit zwischen den Paarlingen einer Mustergruppe von je 35 EZ- und ZZ-Paaren erfolgt eine Beurteilung des Erbeinflußes auf die phänotype Varianz der psychomotorischen Individualität. Eine Analyse der Ergebnisse zeigte, daß bei gleichen äußeren Umständen die individuellen Unterschiede der Motorik mehr von Erb- als von Umweltsfaktoren beeinflußt werden, daß die Erbfaktoren aber mit zunehmender Übung allmählich an Bedeutung verlieren.

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