Heritability of Motor Skill

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A total of 22 monozygotic (MZ) and 41 dizygotic (DZ) twin pairs were given 72 trials on
a stabilometer balance task over six days to study the extent of the genetic contribution
to learning and performance of a gross motor skill. The expectations that interindividual
differences would be less for the MZ than for the DZ twins and that intraindividual
variability would not be different between the two groups were supported. Intraclass
correlations were used to provide estimates for the proportions of total phenotypic
variance accounted for by heritability (h^2), systematic environmental variance (E^2),
and nonsystematic environmental effects (e^2). Heritability was found to be low during
the early stages of learning, before it increased to stabilize at approximately 65% for the
remaining practice. E^2 was highest during these early stages (24%), then declined quickly
to stabilize at half that level. Error variance (e^2) constituted the remaining variance. Learn-
ing profiles of the twin pairs were also analyzed, with a greater intrapair resemblance being
found for the MZ twins. The present findings indicate that, for gross motor skills, there is
considerable potential for influencing both the levels of performance (and learning) and
the differences between individuals by judicious use of systematic environmental effects.

Key words: Balance, Individual differences, Motor learning, Motor performance, Motor skill, Twin
correlations, Analysis of variance

INTRODUCTION

The extent to which inherited characteristics contribute to individual differences in human
behaviour has been studied widely over the past few decades. One method of study was
to observe characteristics prevalent among family members. For example, Gedda et al
[6] examined data on the families of some athletes who competed in the Rome Olympic
Games and concluded that at least part of their specific physical and psychological
qualities could be attributed to heredity. The difficulty with this technique is that it is
descriptive only and lacks quantification.

A second method for studying the relative effects of heredity and environment has
been to use intrapair correlations. Shields, for example, found the average correlation for
height to be r = 0.96 for monozygotic (MZ) twins reared together and r = 0.82 for those
reared apart. For weight, the respective correlations were 0.80 and 0.87 [20]. Jensen re-
ported correlations of 0.94 and 0.96 for height of MZ twins reared apart and reared to-
gether, respectively, as compared to 0.47 for dizygotic (DZ) twins reared together [11].
Burt reported similar figures, as well as considerably lower correlations in DZ than MZ
twins, for a number of physical characteristics [4].

The third method involves the concept of "heritability" and allows estimation of the proportion of the variability that may be assigned to genetic causes. Several methods of estimating heritability have been proposed, and some are widely used. Most have been found to be inadequate, however, and Jensen [10] provided a generalized formula from which the following linear model is derived:

$$V_P = V_G + V_E + 2 \, Cov_{GE} + V_{GE} + V_e \tag{1}$$

where the phenotypic variance (V_P) is accounted for by both genotypic (V_G) and environmental (V_E) sources of variance, as well as by genotype-environment covariation (Cov_{GE}) and interaction (V_{GE}). The final term (V_e) is the variance due to errors of measurement. If it is assumed for the moment that the effects of the covariance and interaction terms are negligible, and we divide Eq 1 through by V_P, the model can be expressed as:

$$1.00 = h^2 + E^2 + e^2 \tag{2}$$

where: h^2 = heritability (V_G/V_P), E^2 = systematic environmental variance (V_E/V_P), and e^2 = unsystematic environmental variance (V_e/V_P). Because V_G itself consists of three components that represent additive, dominance, and interactive effects of genes, the weighted average of these components must enter into the computations for h^2, E^2, and e^2. This complex quantity is represented as ρ and may be described as the genetic correlation one would expect between siblings. While ρ is not known precisely, its value should be close to 0.5 [10, 11]. Thus, the estimate of heritability from comparing MZ and DZ twins is:

$$h^2 = \frac{r_{MZ} - r_{DZ}}{1 - \rho} \tag{3}$$

The proportion of total variance that is caused by systematic environmental variance is:

$$E^2 = \frac{r_{DZ} - \rho r_{MZ}}{1 - \rho} \tag{4}$$

and the proportion due to unsystematic environmental variance is:

$$e^2 = 1.00 - h^2 - E^2 \tag{5}$$

(which is equivalent to $e^2 = 1 - r_{MZ}$).

Review of Motor Skill Studies

One of the earliest studies of *fine motor skill* was conducted by Holzinger [9] who included a tapping task in a battery of other tests. He found that the MZ intrapair correlation for tapping speed was almost twice that of the DZ twins (0.69 vs 0.38). In a related study, Newman et al [18] indicated that performance on tapping speed, card sorting, and pursuit rotor tasks had a clear hereditary component. More recently, Sklad [22] found h^2 coefficients for the tapping task of 0.30 to 0.58.

An important study of the heritability of fine motor skill was that conducted by McNemar [17] who tested 47 MZ and 46 DZ pairs on five different tasks (pursuit rotor, arm steadiness, speed drill, spool packing, card sorting). He found consistently higher intra-pair correlations for MZ than for DZ twins (0.71 to 0.95 vs 0.39 to 0.56). For the card sorting task, McNemar's data yielded an h^2 value of 0.43 for both initial and final stages of practice [24], whereas Vandenberg [23] reported $h^2 = 0.61$ for his study of the same task. The respective figures for the pursuit rotor are $h^2 = 0.79$ (initial) and 0.68 (final) for the McNemar study and $h^2 = 0.52$ for the Vandenberg study [23]. In comparison, a recent study by Marisi [16] reports that h^2 decreased steadily from 0.79 to 0.35 over 30 practice trials and, after a 30 min rest period, a similar result was found when h^2 declined from 0.99 to 0.59.

Other studies of fine motor skills have provided varied findings. For example, although Vandenberg [23] found $h^2 = 0.70$ for the mirror tracing task, Sklad [22] reported values of 0.52 and 0.94 for females and males, respectively. In general, it appears that, while most investigators find higher intraclass correlations for MZ than for DZ pairs, estimates of heritability for fine motor skill vary considerably.

A similar conclusion may be reached in examining the literature for *gross motor skill*. In studying general activity levels, for example, heritability coefficients of 0.40 [19] and 0.67 [23] have been reported. In a ball throw test for accuracy, Sklad [22] found h^2 = 0.87 (female) and 0.40 (male), whereas in a medicine ball throw for distance, Kovar [15] found $h^2 = 0.60$. For a coordination test, vertical jump and shuttle run, Kovar reported h^2 values of 0.48, 0.86, and 0.90, respectively. In other studies of running ability, Sklad [21] found considerably higher correlations in MZ than in DZ twins for the 60 metre dash, whereas Klissouras [14] had similar results for the 1,000 metre run.

Heritability of gross body balance ability has been estimated to be 0.48 for a beam balance task [23] and 0.46 for a ladder climb task [28]. However, Vandenberg [23] found $h^2 = 0.24$ for a body sway test. As in the case for fine motor skill, it is evident that, although there is a relatively broad range of heritability estimates, there appears to be at least a moderate genetic contribution to individual differences in gross motor ability.

It is noteworthy, however, that few h^2 values have been calculated according to the formulae derived from the linear model outlined previously. Moreover, the consequent lack of information to be derived from partitioning the remaining environmental variance into systematic and unsystematic components has been a disadvantage.

Another feature of these studies is that the relatively few that have examined the effects of learning on heritability provide varied findings. For example, in a reanalysis of Brody's data [3] on a test of mechanical ability, Wilde [26] found h^2 to be of about 0.30 for the first trial and to decrease sharply to approximate zero over the next few trials. In contrast, McNemar's data on the spool packing and card sorting tasks provided higher h^2 coefficients that were essentially no different between early and final stages of practice; yet, for the pursuit rotor, h^2 was lower for the final practice session [24]. Marisi [16], also showed decreases in heritability with practice on the pursuit rotor and, in addition, he found that the contribution of systematic environmental effects (E^2) increased as practice progressed, whereas error variance (e^2) remained relatively stable. Although these findings are in general accordance with McNemar [17], it should be noted that interpolation of the 30 min rest could have introduced confounding effects of reminiscence and warm-up decrement in the postrest results [1].

Learning trends were examined in detail by Sklad [22] and, although h^2 was not calculated according to the linear model and the numbers of twin pairs in each subsample were small, the study is noteworthy. Sklad identified three learning-curve parameters for

each subject and found considerably higher correlations in MZ than in DZ twins for the two parameters specifying rate and level of learning. Although h^2 for these parameters were not calculated, the results indicate that individual differences in the trends of performance improvement we call learning are due in part to differences in genotype.

Aim

The present study used a gross body balance task to examine the extent to which individual differences characterize MZ and DZ twins. In addition, it was proposed to estimate h^2, E^2, and e^2 according to their derivations (Eq: 3, 4, 5) from the basic linear model given in Eq. 1. A further purpose was to obtain a large number of repeated observations in order to study the effects of practice on heritability and on the components of environmental variance. Specifically, the expectations and hypotheses may be stated as follows:

1) It is expected that, although the overall performance trends will not differ between MZ and DZ groups, the group measure of interindividual differences (S^2_t) will be smaller for the MZ than for the DZ group.
2) It is hypothesized that no differences for intraindividual variance (S^2_i) will be found between MZ and DZ groups, since there is no reason to assume any differential effect for within-individual consistency.
3) On the basis of the limited evidence available, it is expected that heritability for gross body balance will be in the order of 50%. However, no firm expectation can be given for the patterns of h^2, E^2, and e^2 over continued practice, except that e^2 should remain relatively stable.
4) A particular focus will be on the intrapair resemblance of learning trends over trials, and it is expected that this will be greater for the MZ pairs than for the DZ pairs.

APPARATUS AND METHODS

The sample consisted of 126 twin subjects (59 M, 67 F), volunteer students from 14 urban intermediate and high schools, aged 11.5–18.25 years (m = 14.5, SD = 2.12). The determination of zygosity was done for the 42 same-sexed pairs after all subjects had been tested on the motor task. This was first based on dermatoglyphic analysis, following Holt's method [8], whereby a difference exceeding 50 ridges in the total finger ridge count classes a twin pair as DZ, and then on the questionnaire method [5], which has been reported to be 98% accurate in determining MZ pairs. Since these two methods clearly diagnosed 16 same-sexed pairs to be DZ, blood group analysis (ABO, MN, Rh, Kell) was used to confirm zygosity for the remaining 26 same-sexed pairs.

The apparatus used was a stabilometer similar to that described in detail by Bachman [2], except that, in the present case, the rotation axis of the horizontally pivoted platform was centered through the platform rather than above it. In addition, the present range of movement was $\pm 20°$ from the horizontal, and movement of the platform was measured by a photoelectric pulse-generating system, which provided 1 "movement unit" for each ¼ deg of motion. The subject's stance was with the feet at shoulder width, the legs only slightly bent, with hands on hips and the eyes looking directly ahead. The starting position was alternated by having either the left or the right side of the platform down. The task was to maintain a state of balance at any point along the movement arc. Auditory feedback was provided by a small amplifier and speaker connected to the photoelectric pulse generator, so that a "whirring" noise accompanied large movements of the platform, with more intermittent pulses resulting from small movements.

Subjects were given 12 trials/day for six days. Each trial was for 30 sec with a 30-sec intertrial rest interval. Following each day's session, subjects were instructed to avoid thinking about the task, and it was emphasized that it should not be discussed with their twin or with anyone else.

RESULTS AND DISCUSSION

Figure 1 provides a comparison of performance for MZ and DZ twin groups over the six days of practice. It is clear that the two groups were similar, in that they improved steadily as practice progressed. Moreover, the trends are in close agreement with other studies in which this apparatus was used. Welch and Henry, in particular, have described such trends in exponential terms, which are characterized by a fast learning component over the first 20 or so trials, followed by a slower learning component over the remaining trials. The slightly poorer performance over the initial trials of subsequent days is a typical finding that may be attributed to a "relearning" process [25].

Since the subjects included members from both sexes, it was necessary to see if this resulted in performance differences. Accordingly, t tests for mean performance were conducted among the four subsamples (twin group × sex). None of the tests achieved significance (the t values ranged from 0.42 to 0.51), and the full subject samples were retained without any further analysis by sex.

The pattern of interindividual (S_t) and intraindividual (S_i) differences over adjacent trials for the twin groups are shown in Figure 2. With the exception of the first few trials for S_t, the curves are again similar to those found by other investigators [eg, 25]. It is apparent that the values for S_t are consistently lower for the MZ twins than for the DZ twins. When tested by the F ratio, S^2_{tDZ}/S^2_{tMZ}, the effect was found to be significant for each day. This result confirms the expectation that, although the measure of interindividual differences can be taken only as a general indicator of resemblance (since it deals with differences across all members of a subgroup rather than with intrapair differences), it would nevertheless show that, overall, the MZ group would show less between-individual difference than the DZ group. Moreover, this finding indicates that heritability estimates based on these data will be significant.

As expected, the data in Figure 2 show no differentiation between twin groups for within-subject consistency (S_i).

The possibility that the decreasing patterns for S_t and S_i might have been caused by the pattern of performance scores was examined by dividing these sources of variation by mean performance to provide relative variation. Figure 3 shows that the performance scores clearly were not responsible for the trends in Figure 2, since relative variation increases. These results are in close accordance with those of Welch and Henry [25].

The present data were also analyzed with a split-plot repeated measures ANOVA [13: 245−283]. This ANOVA is a mixed design, with the two main effects being Class and Trials. Subjects were nested as twin pairs under Class. An advantage of this design is that it takes repeated observations (trials) into account and allows evaluation of their effect, as well as that due to the interaction of class and trials. In addition, it permits calculation of an intraclass correlation (that is exactly equivalent to that provided by the one-way ANOVA) using the following relationship of variance components:

$$R = \frac{\sigma^2_c}{\sigma^2_c + \sigma^2_{s\,(c)}} \tag{6}$$

where R is the intraclass correlation, σ^2_c is the variance due to classes and $\sigma^2_{s\,(c)}$ is the variance due to subjects nested under classes.
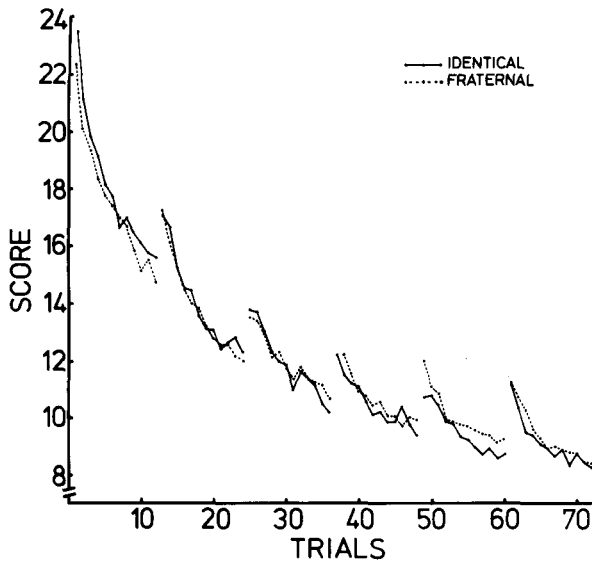
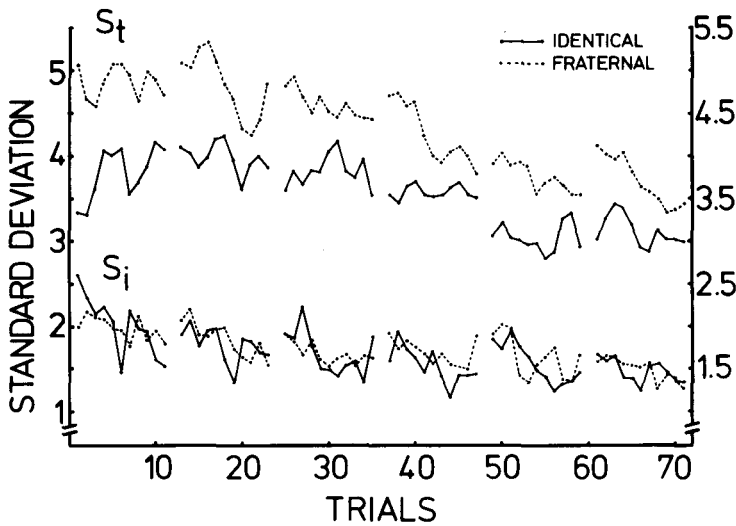Fig. 1. Mean performance scores on the stabilometer for MZ and DZ twin groups over six days of practice.

Fig. 2. Interindividual (S_t) and intraindividual (S_i) variability for MZ and DZ twin groups over six days of practice.
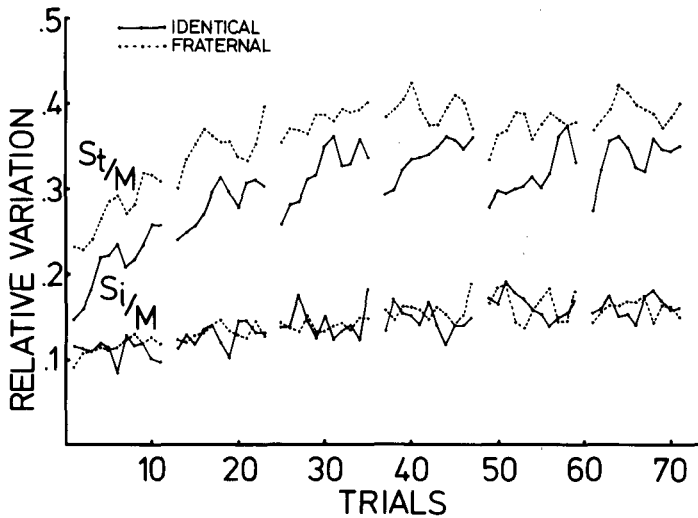
Fig. 3. Relative variation for MZ and DZ twin groups over six days of practice.

This two-way ANOVA was calculated separately for each twin group for each day of practice and also for all six days combined. As expected, the trials effect achieved significance in every instance and, taken over all trials, it contributed an average of 7.2% of the total variance. The MZ intraclass correlations ranged from $r = 0.51$ to $r = 0.78$, whereas for the DZ twins the range was 0.28 to 0.36 (Table).

In considering heritability as it is derived from the linear model, it was assumed that covariation between genotype and environment (Cov_{GE} in Eq. 1) was zero. However, an estimation of the genotype by environment interaction (V_{GE}) was made using the method prescribed by Jinks and Fulker [12], where the sums of the mean scores for all twin pairs (which reflect genotype values) are correlated with the difference scores for all twin pairs (which reflect nongenetic values). Although the MZ group showed the larger interaction, it was not significant and accounted for less than 1.5% of the total variance. Thus, the calculation of heritability on the basis of the simple additive model of genes plus environment appears justifiable.

The results for h^2, E^2, and e^2 are given in the Table and are illustrated in Figure 4. It can be seen that heritability was low on the first day of practice (27%), then it increased to 70% on day 2 and remained close to this level for the rest of the practice. Error variance was also relatively stable over days 2–5, with a higher value for day 1. As a result, the systematic environmental effects were slightly higher on the first day (24%), with an average of approximately 12% over the remaining days.

The present results differ from those of Marisi [16] and McNemar [17], who found that heritability consistently decreased as practice progressed. In particular contrast is the present low value of 0.27 for day 1 as compared to 0.79, which was found for the early stages of practice in both of the other studies cited. In a similar way, the patterns for E^2 do not agree. The present data indicate that the genetic contribution to individual differences is strongly overshadowed by the specific environmental effects of the early learning situation. This may well be a characteristic of a relatively open task such as on the stabilo-

TABLE. Intraclass Correlations (R) and Estimates of Heritability (h^2), Systematic and Nonsystematic (e^2) Environmental Variance for Each Day's Practice and Overall Practice Trials[a]

Day	R_{MZ}	R_{DZ}	h^2	E^2	e^2
1	0.511	0.330	0.274	0.236	0.489
2	0.735	0.276	0.695	0.040	0.265
3	0.696	0.329	0.556	0.140	0.304
4	0.746	0.308	0.664	0.082	0.254
5	0.766	0.335	0.653	0.113	0.234
6	0.781	0.362	0.667	0.114	0.219
1–6	0.748	0.341	0.617	0.131	0.252

[a]A value of $\rho = 0.34$ was used in calculating h^2.
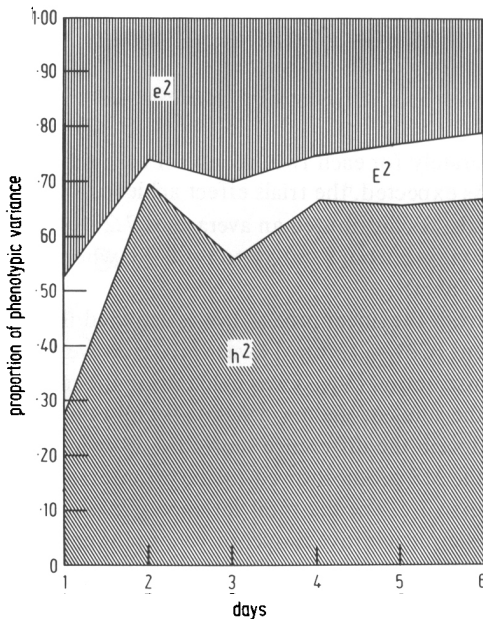

Fig. 4. Comparison of the proportions of total phenotypic variance accounted for by heredity (h^2), systematic environmental variance (E^2), and error variance (e^2).

meter, where the subject is faced with a relatively continuous task involving the maintenance of balance on a very unstable base and where auditory feedback provides additional information. In contrast, the pursuit rotor has a more closed environment, since it involves tracking an experimeter-paced target that moves at a predetermined speed in a constant direction.

Although the foregoing results provide an indication of the relative contribution of genotype to individual differences in performance, the contribution to learning is less clear. If heritability contributes significantly to individual differences in learning, then

the learning curves of the MZ pairs should be more alike than those of the DZ pairs. One method of examining this question would be to compute an intraclass correlation (R_{ck}) from the class-by-trials interaction provided by the two-way ANOVA, and to calculate the overall resemblance for each twin group as $1 - R_{ck}$ [7] . However, with learning tasks such as the stabilometer, this technique may have limited use, since under normal conditions the learning profile usually follows a very systematic exponential form, with individuals becoming more alike as practice proceeds [25] . As would be expected from the present data, no significant class-by-trials interaction was found, which indicates that the between-pair learning profiles were essentially similar.

Thus, a closer consideration of the question of the contribution of genotype to individual differences in learning may be made by examining the within-pair differences in learning profiles; and although this would not allow the calculation of a meaningful heritability coefficient for learning, it should provide a useful comparison of the two twin groups. Accordingly, the within-pair correlations for the learning profiles over all 72 trials were calculated for each twin pair, and with a z-score transformation, the general profile correlation (R_p) was determined for each twin group. The correlations provided by this analysis were $R_p = 0.696$ for the MZ twins and 0.612 for the DZ twins and indicate that the intrapair resemblance of the learning profiles over all 72 trials was 12% greater for MZ twins. This result is in general agreement with the findings of Sklad [22] .

CONCLUSIONS

The present findings indicate that during the early stages of practice, when learning is rapid, heritability is low; thereafter, it quickly reaches a relatively stable level that accounts for approximately 65% of the total variance.

In contrast, the systematic effects from the environment contribute more during the early phases (24%) and then reduce to stabilize at around 12%. Therefore, apart from the initial stages, these two major components account for almost 80% of the total phenotypic variance (with the remainder being error variance).

These findings indicate that there is considerable scope for manipulating environmental conditions to change the level of performance and learning. Although such manipulation might not have much influence on individual differences if heritability were in the order of 95% or more, the present findings suggest that individual differences can be influenced by environmental conditions. The greatest potential for such influence appears to be during the early stages of learning.

It is evident that if we can systematically account for the major sources of variance in the different types of motor skills, then it should be possible to determine those classes of variables and conditions that will facilitate developmental and educative processes in motor skill.

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