Vassilis Klissouras and Dan Q. Marisi*

Genetic Basis of Individual Differences In Physical Performance

If a man does not keep pace with his companions, perhaps it is because he hears a different drummer. Let him step to the music which he hears, however measured or far away.

—Thoreau

The phenomenon of human diversity which has been empirically observed and verified, has long attracted considerable attention among educators and researchers. The fundamental reasons for the expressions of variance in human endeavors are inextricably linked to both genetic predisposition and environmental influences. That is, the phenotypic expression of an individual's motor ability, structural dimensions and physiological capacities is not solely and unalterably set by his genetic constitution, but is also affected by environmental forces. In this respect, the frequently raised question "Is a superior athlete born or made?" is meaningless. It is not a dichotomy of predetermination versus plasticity. The gene constellation that each individual possesses cannot operate in an environmental vacuum, but in fact must act in concert to provide an optimal condition for phenotypic expression. Thus, the question more appropriately phrased would be, "To what extent are individual differences in performance determined by genetic factors, and to what degree by nongenetic factors?"

Evidence from genetic research is needed not only because of its theoretical importance, but also because of its pedagogical implications. Heritability should be of interest to educators since the degree

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to which we can influence the expression of the genotype depends to a considerable extent upon our knowledge of its relative strength. That is, the magnitude of the extragenetic component may provide an indication of the proportion of variation in abilities we potentially can modify by educational and social-psychological means. Further, acquisition of such knowledge may warrant a critical synthesis of some of the fundamental premises on which contemporary sport is based. Furthermore, it may demonstrate the actual potential of physical activities and enable the educator to place objectives in perspective and to realize what he can and cannot achieve through the medium of practice and exercise. Obviously, the information obtained from genetic studies has practical importance in the selection and training of athletes for different sports.

genetic factors in functional capacity

Wide interindividual variability exists in functional capacity and one wonders to what extent individual differences are attributable to genetic endowment and to what extent to environmental conditions. A statistical comparison of the intrapair differences between identical and nonidentical twins may provide an answer to this question since phenotypic variability in identical twins is due solely to environmental agents, whereas that in nonidentical twins is due to both genetic and extragenetic influences. In a study (10) based on such a comparison of intrapair twin differences it was observed that the contribution of heredity to the interindividual differences in maximal oxygen uptake (a performance criterion of functional capacity) was relatively high. *Figure 1* depicts the data obtained from 15 pairs of Monozygotic

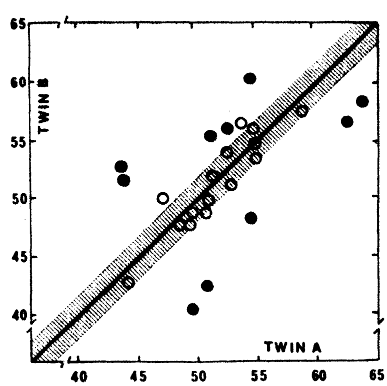

Figure 1: Intrapair values of maximal oxygen uptake for identical (○) and non-identical (●) twin boys aged between 7 and 13 years (Data from ref. 10).

(MZ) twins and 10 pairs of Dizygotic (DZ) twins. It may be observed that the intrapair differences tended to be smaller between identical twins than between nonidentical twins to the extent that experimental error could account for the magnitude of the intrapair differences in identical twins.

Statistical treatment revealed that the difference between MZ and DZ twins, in terms of intrapair variance, was significant well beyond the 0.01 probability level. It should be noted that relatively young twins were used as subjects in this study to ensure that environmental influences were similar for both groups of twins. It was hypothesized, however, that DZ twin pairs would be under more diverse environmental influences than MZ twin pairs at later stages of physical development.

In twins exposed to similar environments at different stages of their lives, any meaningful differences between dizygotic as compared with monozygotic twins must be an expression of the relative strength of the genotype. In those twins exposed to contrasting environments, the resulting differences may provide a measure of this responsiveness to environmental forces. Thus, a follow-up study was conducted to determine whether the small intrapair differences observed between identical twins and the marked differences between nonidentical twins would persist throughout life (11). Thirty-nine pairs of twins (23 MZ and 16 DZ twins of both sexes), ranging in age from 9 to 52 years, were used as subjects in the study. The results shown in *Figure 2* supported the conclusion that heredity accounted almost entirely for existing differences in maximal oxygen uptake.

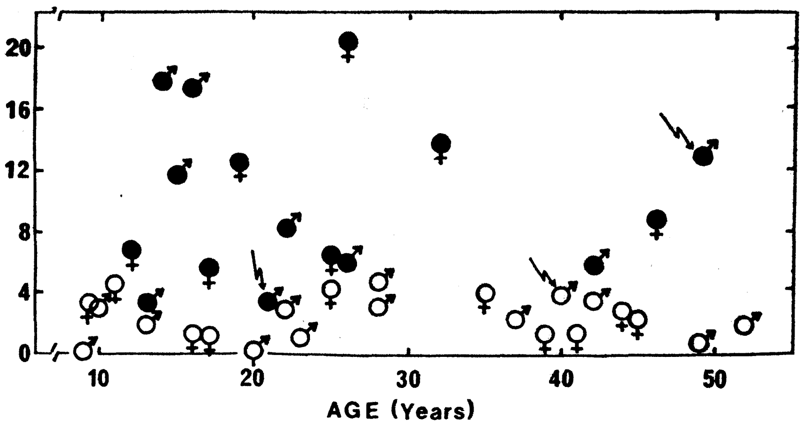

Figure 2: Intrapair differences in maximal oxygen uptake in identical (○) and non-identical (●) twins of different age. Arrows indicate three case studies discussed in the text (Data from ref. 11).

One may still wonder whether intrapair differences in maximal oxygen uptake could possibly be related to differences in mode of life. In a case study (11) of a pair of nonidentical twins (21 years of age) who had been separated for 5 years, it was observed that one twin had trained strenuously for competitive middle distance running, whereas his brother had never participated in sports of any nature. It was therefore surprising to find that the untrained twin had a maximal oxygen uptake of 56 milliliters per kilogram of body weight per minute (ml. kg^{-1}. $min.^{-1}$) as compared with a value of 53.0 for his trained counterpart. One cannot escape the inference that if it were not for the physical training, the intrapair difference between this twin pair may have been greater. Further, the implicit postulate of this observation is that those individuals with an inferior genotype must be exposed to a greater amount of physical activity in order to attain an average adaptive value, whereas those with generous native endowment may not need more than a threshold exposure to maintain their high adaptive value.

Two other case studies proved to be intriguing. In one situation, two identical twin brothers, 40 years of age, had been separated at age 12 and had had different lifestyles. More importantly, one twin had engaged in vigorous training for competitive basketball at the national level whereas his brother was only moderately active during the same period. For the last ten years neither of them had been involved in regular physical exertion. When tested, their maximal oxygen uptake values were very similar — the absolute values being 38 and 42 ml. kg^{-1}. $min.^{-1}$ for the trained and untrained twin respectively. In another case, a pair of nonidentical twins had maximal oxygen uptake values of 32 and 45.0 ml. kg^{-1}. $min.^{-1}$ when tested at 49 years of age. They had lived together all their lives, had the same profession and both played competitive soccer from early childhood until they were 22 years of age. These observations support the notion of the prepoderance of natural tendency advanced by Galton (34):

> Many a person has amused himself by throwing bits of stick into a tiny brook and watching their progress; how they are arrested, first by one chance obstacle, then by another and again, how their onward course is facilitated by a combination of circumstances. He might ascribe much importance to each of these events, and think how largely the destiny of the stick had been governed by a series of trifling accidents. Nevertheless all the sticks succeed in passing down the current, and in the long run, they travel at nearly the same rate. The one element that varies in different individuals, but is constant in each of them, is the natural tendency; it corresponds to the current in the stream, and inevitably asserts itself.

environmental influence in functional capacity

The potency of environmental forces upon hereditary predisposition can be fully evaluated only if they are given a chance to act maximally. In this context, it is important to know the limits set by the genotype, the relative potency of training at different developmental ages and the extent to which genotype and training stimuli interact. The answers to these questions can be elucidated with analyses of data from twin studies, where each subject is matched to his genotypically identical control.

"Ceiling" of Performance. All functional capacities and physiological processes in man, as in all species, have a genetically determined ceiling of performance. For example, the upper limit of values for oxygen uptake is a little over 7 litres/min. and that of cardiac output close to 40 litres/min. Additionally, we find that ceilings characteristic of individual genotypes must exist at different levels (1) and the question then arises as to what extent environmental influences, such as physical training, can raise an individual's capacity towards the species' maximum value.

To obtain some insight into this question, a trained athlete and his untrained twin brother were tested over a period of 1½ years (12, 13). The untrained twin had a $\dot{V}O_2$ max of 36 ml. kg^{-1}. min^{-1}, whereas the trained twin had a peak value of only 49 ml. kg^{-1} $min.^{-1}$. This latter value, well below values reported for top athletes, is comparable to a value of about 50 ml. kg^{-1} min^{-1} for untrained college men of the same age. Thus, despite hard and prolonged training, the trained twin was unable to surpass an average level of adaptive capacity. The reason for this seems to hinge on his low pretraining functional adaptability as judged from that of his identical brother. This observation strongly suggests that rigorous athletic training cannot contribute to functional development beyond the limit set by the genotype.

In view of the empirical evidence, it would appear that *not* all individuals possess the genetic potential which, with appropriate training, can find phenotypic expression in superior athletic achivement.

Early Training. There is much speculation, but little evidence, regarding the relative potency of training at different developmental ages. A recent study (33) involving 12 pairs of identical twin boys (4 sets aged 10 years, 4 sets aged 13 years, and 4 sets aged 16 years) was designed such that one twin trained, while his identical brother served as a control and continued in his normal day-to-day activity pattern. The training program was of a ten-week duration and was designed primarily to improve the subject's endurance by both interval and continuous exercise. The percentage intrapair differences for maximal oxygen uptake before and after training is shown in *Figure 3*. The mean intrapair difference was 11.5% and 14% for the 10 and 16 year old groups respectively but it was not appreciably different in the 13 year olds.

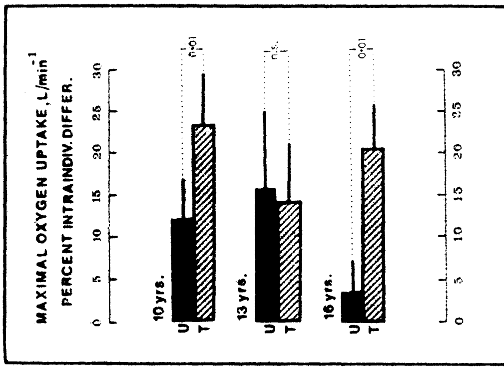

Figure 3: Mean percent difference, standard deviations and significant levels of maximal oxygen uptake for untrained (U) twins and their trained (T) brothers of three age groups (Data from ref. 33).

Since the type, intensity, duration and frequency of exercise was the same for all groups, the reason for this difference in response should be sought for in factors other than training. The most likely explanation for the commensurate increase in $\dot{V}O_2$, in both trained and untrained 13 year-old twins, seems to hinge on the influences associated with the adolescent growth spurt that occurs at this age and is assessed by the height velocity. It is possible that hormonal activity is optimal during this age and any additional stimuli such as training cannot override its influence. In this connection, one thinks of the anabolic activity of the growth hormone, which stimulates the transport of amino acids across cell membranes and the synthesis of protein. However, some other factors must play an essential role, since the blood growth hormone levels in children and adolescents are not different from those observed in adults during rest and in response to muscular work.

The question still remains: At which developmental period is exercise most effective? Poupa and co-workers (25) induced experimental cardiomegaly in rabbits and observed that animals in which the cardiomegaly was induced at an early age responded with an increase in the oxygen-consuming structures of the myocardium (cardiac cells) and the oxygen-supplying structures (terminal vascular bed per weight unit of cardiac tissue), whereas overloading of the heart during adulthood evoked development of the former structures, but not of the latter ones. Thus, they concluded that the ability of the heart to respond to the need for increased functional capacity is limited to the early post-natal period. The corresponding developmental period in man is not certain.

It is evident that the ontological time factor is decisive in the development of functionally important structures. However, it still remains uncertain at which developmental period the growth-promoting simuli which act upon the tissues should be applied. The old hypothesis that more might be gained by introducing extra exercise at the time when the growth impulse is the strongest is no longer tenable in view of the present evidence.

Genotype-Training Interaction. A question of considerable theoretical and practical importance is whether different genotypes respond to a given training stimulus with a change of different magnitude. Split-twin experiments, in which one twin trains and his identical partner acts as a control, make it possible to separate the observed intrapair variance into its three components: that due to heredity, that due to training and that due to the interaction between heredity and training. Eight twin boys underwent a 10-week training program of the same amount and intensity, while their identical brothers restricted their activities to normal daily routines (33). The $\dot{V}O_2$ max of all twins was measured before and at the end of the 10-week period. The mean $\dot{V}O_2$ max for all experimental and control twins was 51.9 ml. kg^{-1} min^{-1}, with nonsignificant intrapair differences. The interpair variability ranged from 41.1 to 58.6 ml. kg^{-1} min^{-1}, so that the interaction hypothesis could be tested. The mean $\dot{V}O_2$ max after training was 59.4 ml. kg^{-1} min^{-1}, with adjustments for changes observed in the non-trained twins, and the range was 45.2 to 69.3 ml. kg^{-1} min^{-1}. Treatment of the results with the analysis of variance revealed that the interaction between genotype and training does not contribute significantly to the total variance.

These findings do not support the notion that the magnitude of improvement in $\dot{V}O_2$ max depends on the relative strength of the genotype. Thus, the inverse relationship occasionally observed between initial level of $\dot{V}O_2$ max and relative improvement should be attributed to the amount and intensity of physical activity which presumably modifies the initial level of $\dot{V}O_2$ max. Further, it is surprising to find that in spite of strenuous training, the main cause of the total variance in $\dot{V}O_2$ max is still the genetic predisposition.

heritability estimates in motor performance and anthropometric dimensions

The extent to which genetic predisposition accounts for interindividual variation in a given attribute is commonly expressed by the heritability index. If the heritability index is unity, then the heredity may be considered the cause of the observed variation. If the coefficient is zero, the variation may be attributed solely to environmental influences. If the variation is partly affected by environment and partly conditioned by heredity, the index will fall between these two extremes and its proximity to unity is an indication of the relative strength of the genotype.

Motor Performance. Heritability coefficients are presented for selected motor variables in *Figure 4*. Although there is some scatter of the heritability and the correlation coefficients reported by different investigators, there is general agreement that identical twins are significantly more similar than fraternal twins in motor development (6, 23) and motor ability (14, 15, 16, 17, 20, 26, 32). Moreover, it seems that simple and phylogenetic motor activities, such as walking, are more conditioned by heredity than complicated and ontogenetic activities, such as throwing and balancing (6, 23).

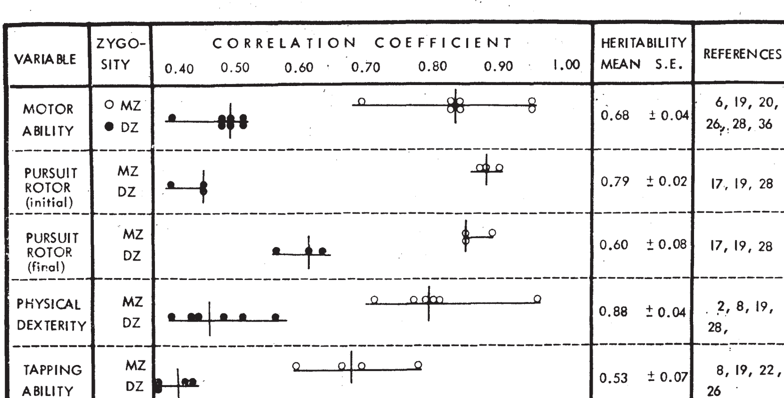

Figure 4: Correlation and heritability coefficients for selected motor variables. The median values of the correlation coefficient are shown by vertical lines intersecting the range of values. Heritability estimates, where not reported, were calculatd by Holzinger's formula.

A few authors have suggested that since practice of ontogenetic type of tasks appears helpful only when the organism is maturationally prepared, the effects of heredity may be centered on the developing neural structures rather than on motor abilities. In this way, heredity may exert more of a mediating, rather than direct, influence on motor development through its effect on the development of neural maturation.

Gedda (5) has assumed that individual sports aptitude depended on an exogenous factor, or environmental conditions such as training, and an endogenous factor which refers to the transmitted characteristics necessary for the acquisition of skill in a specific sport. He noted identical twins are more likely to participate in similar sports than nonidentical twins and he ascribed this observation to the inheritance of a particular sport phenotype within certain families. On the basis of these studies Gedda concluded there was a hereditary basis in sport activity and that theoretically, a specific sports genotype is transmitted as a dominant. Similarily, Grebbe (7) concluded that sporting ability depended on hereditary factors caused by the action of many independent genes.

It is reasonable to attribute, therefore, individual differences in motor performance to heredity. However, although achievement in athletic pursuits may ultimately be determined by the genotype, environmental experiences can influence the level of achievement. Even the most favorably endowed individual, unless his energies are directed in a constructive manner and his abilities developed through instruction and practice, will not attain a superior level of performance. The inheritance of specific abilities simply facilitates the acquisition of motor skill — but does not assure it.

The findings of most genetic studies dealing with motor performance report a greater degree of resemblance for identical twins than for fraternal twins. The data from three independent studies (17, 19, 35) also indicated that practice on a particular task tended to increase fraternal twin-pair resemblance whereas the resemblance between identical twin-pairs was essentially unaffected by practice. A similar interpretation was offered by Brody (2) with respect to mechanical ability. This observation would reinforce the contention that high heritability by itself does not necessarily imply that a particular characteristic is immutable since the strength of the genetic control has been shown to diminish systematically throughout the course of practice obeying a monotonic trend over trials (*Figure 5*). A recent study (18) has estimated the extent of the genetic control to individual differences in the rate of learning a motor task. The results indicated that approximately half of the total variance for rate of learning was attributable to genetic causes.

In light of the findings reported in the literature, it would appear that the substantially greater contributory component of persistent individual differences in motor behavior is due to an individual's genetic endowment.

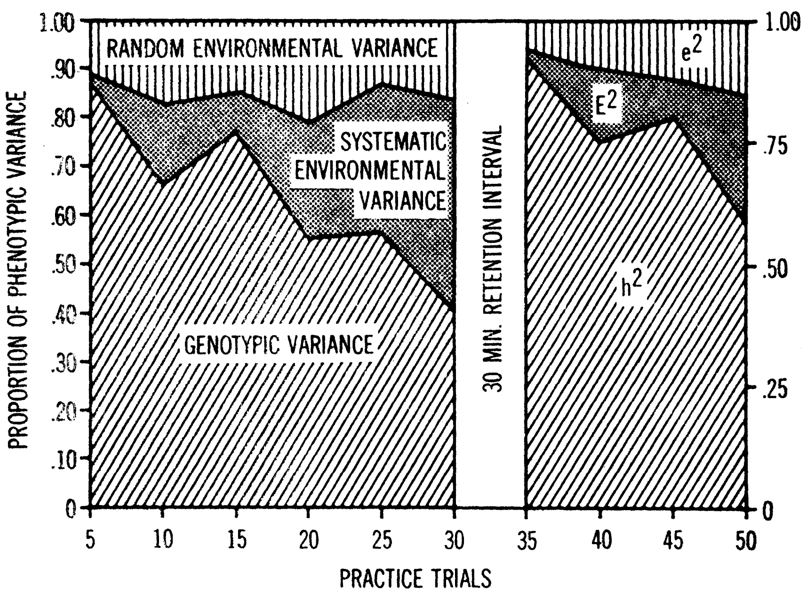

Figure 5: Proportion of total true-score phenotypic variance ($_\rho p^2$) accounted for by heredity (h^2), between-families environmental variance ($_\rho E^2$), and within-families environmental variance ($_\rho e^2$) (Data from ref. 17).

Anthropometric dimensions. It is reasonable to assume that an individual's functional capacity and motor performance are related to his structural dimensions. The most characteristic thing about anthropometric components of physique is that they are distributed in the adult population continuously and unimodally. Measurements of breadths and depths depart somewhat from normality in the direction of platykurtosis and positive skewness, but the departure is not very great and seems to depend primarily on the distribution of subcutaneous fat. This interindividual variability in human physique is attributable to genetic and nongenetic causes.

Some morphological characteristics such as body weight and limb or trunk circumference are obviously more liable to modification and support by environmental means than other measures. For example, it has been reported (31) that the influence of environmental factors such as nutrition and exercise has promoted a height differential of two inches in favor of first generation Japanese immigrants over their former countrymen. That is not to imply, however, that anthropometric variability is solely conditioned by environmental agents. Rather, it is convenient to envisage a continuum at one end of which are characteristics in which the genetic component of individual differences is minimal, while at the other end, the environmental component is either absent or minimal. Between these extremes may be noted variables such as height, weight and breadth which, while mainly genetic in origin, are nevertheless subject to environmental modification.

Investigators have sought to estimate the extent of the genetic strength to individual differences in a number of single anthropometric measures, and, in view of the relatively unequivocal conclusions, the formulation of an anthropometric composite, with respect to genetic and nongenetic influence, would appear tenable.

Vandenberg (29) summarized six independent studies showing a broad measure of agreement regarding the heritability of 47 different anthropometric variables. In general, the intrapair variance of identical twins was significantly less than that of fraternal twins for measures of length, whether of the trunk or the extremities. This fact appeared to hold true even for finger and foot length. Other studies (3, 4, 9, 22, 27) support this conclusion and have noted the relative strength of the genetic constitution to interindividual variability in measures of length. To facilitate quantitative comparisons of different studies with regard to various anthropometric measures, where possible, original data were reanalyzed in a uniform manner. The results of this analysis indicated that about 86% of the total variance for measures of body and limb length was genetically determined.

Although primarily controlled by heredity, limb circumference and weight (80%) appear more susceptible to modification by environmental influences whereas measures of physical breadth and depth (83%) are only slightly more influenced by environment than are the length measures. Other measures such as cephalic and facial characteristics, amount of adipose tissue, and bi-trochanteric width are also genetically determined to various degrees. Thus, it would appear that the main differentiating factor in this respect is the importance played by the bone dimension associated with any anthropometric feature. Stature and longitudinal measures of the limbs are mostly bone measurements, as are most cephalic and facial characteristics, whereas limb circumferences and weight have a large fat and muscle component.

summary

In this paper we have tried to present some twin findings and interpret their meaning. These findings were derived from studies which used the twin model and co-twin analysis. In summary we can state that:

a. The genetic factor is the principal determinant of the variability in functional capacity as assessed by the maximal aerobic power observed among individuals regardless of age, who have lived under similar environmental conditions. Further, interindividual differences in physical work capacity, anaerobic capacity, maximal muscular force, reflex time and conduction velocity are also governed by genetic differences, while maximal work ventilation, total lung ventilation, residual volume, forced expiratory volume at 1.0 second, and maximal speed of muscle shortening show almost as much diversity in DZ as in MZ twins.
b. The relative contribution of heredity to the total variance of functional capacity can be reduced to about 50% with the operation of extreme environmental conditions. Habitual exercise can profoundly affect the expression of the genetic potential, but this can occur only within the fixed limits of heredity.
c. The ontological time factor may be decisive in development of functionally important structures, but the old hypothesis that more might be gained by introducing extra exercise at the time when the rate of growth is greatest is not tenable.
d. Within the limitation of a narrow range of genetic variability observed in $\dot{V}O_2$ max, different genotypes respond to a given training stimulus with a change of the same magnitude.
e. A substantially greater proportion of the variability in motor performance is determined by genetic predisposition. The strength of the genetic control of individual differences, however, appears to be inversely related to the complexity of the motor activity.
f. Factors regulating anthropometric expression in terms of height, weight, circumference, breadth, and depth may be considered largely genetically determined.

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