RESUME

Le but de cette étude était d'établir à quel degré l'hérédité contribue aux variations inter-individuelles dans la relation force-vélocité du muscle humain. Plus spécialement, la méthode de recherche a utilisé des jumeaux afin de déterminer l'estimation du facteur hérédité pour: la force musculaire maximale développée par les fléchisseurs de l'avant-bras d'après les courbes force-vélocité de l'individu; la vélocité maximale (V max) de mouvement de l'avant-bras produite par la contraction des muscles sous condition sans charge; et la force isométrique maximale (P_O) produite par la contraction de fléchisseurs de l'avant-bras avec le coude à un angle de 80 degrés par rapport au plan horizontal.

Les sujets étaient des jumeaux de type monozygotique (N = 9 paires) et des jumeaux de même sexe de type dizygotique (N = 8 paires) dont l'âge a varié entre 11 et 17 ans.

Un ergomètre conçu spécialement a servi à déterminer la relation de la force-vélocité des fléchisseurs de l'avant-bras au moment où ils ont déployé leur force dans la paume de la main de façon collective. De la position de départ à 60 degrés par rapport au plan horizontal, chacun des jumeaux a fait une seule flexion maximale volontaire des fléchisseurs de l'avant-bras pendant une série de charges différentes. Le rayon du mouvement était de 50 degrés et chacun des jumeaux a porté des charges identiques avec une période de repos de trois minutes entre chaque épreuve. La force maximale à la paume de la main (kg) et la vélocité

maximale linéaire (m/sec) correspondante furent obtenues avec un déplacement de l'avant-bras de 85 degrés à chaque épreuve.

Ces valeurs obtenues par expérimentation, de même que la vélocité linéaire maximale du mouvement sous condition sans charge (V max) ainsi que la force isométrique maximale (P_0) étaient les points de repère sur lesquels les courbes de force-vélocité de moindre carrés furent établies. Les courbes de la force musculaire maximale (kgm/min) furent calculées d'après ces courbes de moindre carrés.

Les estimations de la variance à l'intérieur des paires furent obtenues à l'aide d'une analyse de variance à un palier pour la puissance musculaire maximale (MMP), la vélocité maximale du mouvement (V max), et la force isométrique maximale (P_0). Si la proportion de variance à l'intérieur de la paire $F = \frac{W^2DZ}{W^2MZ}$ était statistiquement significative, les estimations d'hérédité (H_{est}) furent établies d'après l'équation suivante:

$$H_{est} = \frac{W^2DZ - W^2MZ}{W^2DZ}$$

Une différence significative entre les variances des paires MZ et des paires DZ fut établie en ce qui concerne la puissance musculaire maximale et la force isométrique maximale; la valeur H_{est} se révéla respectivement à 97% et 83%. Cependant, la valeur $F(\frac{W^2DZ}{W^2MZ})$ pour la vélocité maximale du mouvement n'était pas significative et la valeur H_{est} pour cette variable ne fut pas établie. En se basant sur cette analyse, nous concluons que les variabilités inter-individuelles de la relation force-vélocité du muscle humain sont basées presqu'entièrement sur la variation de l'hérédité.

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HERITABILITY OF THE FORCE-VELOCITY RELATION IN HUMAN MUSCLE

by

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ABSTRACT

The purpose of this investigation was to ascertain to what extent variation in heredity contributes to interindividual variation in the force-velocity relation of human muscle. More specifically, the twin study method of research was employed for the purpose of attempting to derive heritability estimates for: the maximal muscular power developed by the forearm flexor muscles as derived from individual force-velocity curves; the maximal velocity of movement of the forearm (V_{max}) produced by the contracting forearm flexor muscles under unloaded conditions and; the maximal isometric force (P_0) produced by the forearm flexor muscles at an elbow angle of 80 degrees with respect to the horizontal.

Male monozygotic twins (N=9 pairs) and like sexed dizygotic twins (N=8 pairs) participated and their ages ranged from 11 to 17 years.

A specifically designed ergometer allowed the determination of the force-velocity relationship of the forearm flexor muscles as they collectively exerted their force at the palm of the hand. From an experimental starting position of 60 degrees with respect to the horizontal, each co-twin pair made a single voluntary maximal flexion of the forearm flexor muscles for a series of different loads. The entire range of movement was 50 degrees and each co-twin pair received identical loads with a three minute rest interval between each load. The maximal exerted palm force (Kg) and its corresponding maximal linear velocity (m/sec) were

obtained at a forearm displacement of 85 degrees for the different loads.

These experimentally obtained values, along with the maximal linear velocity of movement under unloaded conditions (V_{max}) and the maximal isometric force (P_o) provided the reference points on which the "best fit" force-velocity curves were drawn. The maximal muscular power (Kgm/min) curves were calculated from the "best fit" force-velocity curves.

Within-pair variance estimates were generated by a one-way analysis of variance for maximal muscular power (MMP), maximal velocity of movement (V_{max}), and maximal isometric force (P_o). If the within-pair variance ratio $F = \frac{W^2DZ}{W^2MZ}$ was statistically significant, heritability estimates (H_{est}) were derived from the following equation:

$$H_{est} = \frac{W^2DZ - W^2MZ}{W^2DZ}$$

A significant difference between the MZ within-pair variance (W^2MZ) and the DZ within-pair variance W^2DZ was found for maximal muscular power and maximal isometric force and disclosed a H_{est} value of 97% and 83%, respectively. However, the F ratio ($\frac{W^2DZ}{W^2MZ}$) for maximal velocity of movement did not prove significant and the H_{est} value for this variable was abandoned. On the basis of the analysis, it was concluded that the interindividual variability observed in the force-velocity relation in human muscle is governed almost entirely by variation in heredity.

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CHAPTER I

STATEMENT OF THE PROBLEM

Introduction

> "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 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".(21)

This notion of the constancy of heredity, that varied between individuals, and inevitably asserted itself, was advanced by Galton as early as 1875. Today, there is little doubt that hereditary differences have contributed to the existing variability in the mental and physical characteristics of human beings. However, heated debate still remains over the problem of how much of the inter-individual variability is caused by variation in heredity, and how much is caused by variation in environment.

The variability in some characteristics such as eye colour, hair colour, or fingerprints, might be considered to be governed exclusively by differences in heredity, for they are not modified by existing differences in postnatal environment. However, even such traits as these, must have had an appropriate environment during prenatal development in order to express themselves at all. Other characteristics, such as test intelligence, morphological dimensions, and physiological processes, show continuous variation and are known to be markedly influenced by postnatal environment. Such characteristics as these, have offered a favorable opening for an attack on the heredity-environment problem; for the distribution of any given continuous trait for a given population, can be represented by a normal distribution curve.

Galton (21) was the first to suggest that differences and similarities between monozygotic (MZ) and dizygotic (DZ) twins be used as a criterion of the relative powers of heredity and environment. With this is mind, Holzinger (33), contrived the heritability index (h^2), which he described as, "a measure of the relative effects of nature and nurture factors upon the differences found between members of twin pairs reared within a family" (59, p. 111). The heritability index formula was:

$$h^2 = \frac{W^2DZ - W^2MZ}{W^2DZ} \qquad (1)$$

where, W^2 was the within-pair variance of the twins for the trait under study.

Holzinger's heritability index considered only the within-pair variance for the twins and did not take into account the between-pair variance or the interaction effects.

The index has been modified and elaborated by others (7,60, 61, 81), and the word index has generally been replaced by estimate (4,46,47,49,50,56,76,77,78,79,80), but the meaning has remained unchanged. The heritability index, as proposed by Holzinger (33), has signified only a proportion of the total variance in a trait that can be attributed to variation in heredity. Heritability is a useful word, provided this reservation is kept in mind.

Recent attempts that have been made to derive heritability estimates for some physiological variables have utilized Holzinger's index as a basis (4,47,50,51,52,56). These studies have postulated a simple model of the relationship between heredity and environment in order to make the computations behind heritability estimates more explicit. The model has suggested that heredity and environment contribute jointly but independently to all continuous traits, in an additive summation. Further, two basic assumptions must be accepted for the model. Firstly, that the amount of pre and postnatal environmental influence, which has contributed to the total within-pair variance for MZ twins, is comparable to that for DZ twins. Secondly, that the heredity-environment interaction effect has been nil. The heredity-environment model, and the tenability of accepting its underlying assumption, are discussed later in a separate section which establishes the theoretical framework for the present investigation.

Only in the past few years, have physical educators become increasingly aware of the fact that the observed inter-individual variation in many physiological variables may be governed largely by hereditary differences. High hereditary components have been found to contribute to existing differences in cardiorespiratory (4,47,51,82), as well as neuromuscular responses (15,41,50,52,56,57). Since many of these individual differences become accentuated under the influence of exercise, the limit to which an individual may excel in a given athletic event may be "set" by hereditary factors. Therefore, continued research into the extent to which heredity contributes to existing differences of physiological responses to exercise is of utmost practical importance to physical educators. The twin study method will permit a number of these responses to be ranked in order of the contribution of heredity to the total variance in each of those variables. Further, it will allow the eventual prediction of potential performance in athletic events that require the acquisition of specific physiological attributes. A one-kilometer run test, has already been designed to predict potential performance in events that depend upon an individual's maximal oxygen uptake (48).

One physiological response, which is presumed to be the basis of individual differences observed in activities such as sprinting, throwing, and jumping, is the maximal muscular power that can be produced by the contracting muscles. The variability in maximal muscular power has been shown to be governed by differences in the relative position of the force-velocity curve upon which the muscles have contracted (35). The force-velocity curve of contracting muscle, has demonstrated the inverse relationship between the maximal amount of force a muscle can exert, and its maximal velocity of contraction under loaded conditions. The heavier the load that a muscle or group of muscles is made to contract maximally against, the greater will be the exerted force and the slower the velocity of contraction. Conversely, the lighter the load, the less will be the exerted force and the faster the velocity of contraction. When the corresponding force and velocity values, obtained from single maximal muscular contractions for a series of variable loads are plotted, the force-velocity relationship is expressed as a curve (31, p. 137). In addition, the force-velocity values of maximal isometric force (P_0), and the maximal velocity of contraction under unloaded conditions (V_{max}), have provided further experimental points at the extreme ends of the curve (85). The force-velocity curve is always expressed in the same form, that is, as a rectangular hyperbola, though the absolute values of the coordinates on which the curve is drawn may vary with the species examined (22,53), the type of muscle (1,72), and the muscle temperature (28,44).

At least four empirical equations have been proposed to describe the hyperbolic nature of the force-velocity relation of contracting muscle (31, p. 137). A. V. Hill has adapted the simplest "characteristic equation" to the curve which relates the velocity of contraction and the exerted force in a dynamic contraction (28). The equation was:

$$(P + a)\ (v + b) = (P_0 + a)b \qquad \text{(II)}$$

where,

P = the load on the muscle;

P_0 = the maximal isometric force;

a = a constant with the dimension of force;

b = a constant with the dimension of velocity; and

v = velocity of contraction.

For many years, the decrease in exerted force when the muscle was made to oppose lighter loads was attributed to more energy being used to overcome an increased viscosity of the muscle at greater velocities of contraction (6,11,18, 20,22,25,26,30,32,53,54,73,74). However, the experiments by Fenn and Marsh (17), have concluded unequivocally that as the speed of contraction increased, the force decreased, not in a linear fashion as would be expected if viscosity alone was concerned, but rather in an exponential fashion, a small hypothetical correction being made for the true viscosity effect. Fenn stated that "this exponential relation was concerned in some way with the processes of developing extra energy for work of shortening" (17). It is now known, that the diminution of force as the velocity of contraction is increased, is related to a property of the cross-bridges.

As the myofilaments are allowed to move faster, they are less capable of making the cross-bridge connections between the actin and myosin filaments, which are presumed to be the sites of force generation in muscular contractions (34).

The force-velocity relation has been demonstrated in isolated striated muscle (17,28,44), as well as the intact human muscle (9,49,85). The measurement has made possible the determination of the maximal muscular power output, which has been shown to be the product of the force and corresponding velocity values obtained at approximately one-third of their maximum values (27,28,65).

The Problem

From the meager data available, it has become apparent that a wide inter-individual variability exists in the relative position of the force-velocity curve which has been responsible for the existing differences in maximal muscular power output of individuals (35). Further, variability has been demonstrated in the two components that determine the shape of the force-velocity curve at either end, namely, the maximal velocity of contraction under unloaded conditions (V_{max}), and the maximal isometric force (P_o) (9,85).

Komi (50), has recently revealed a very high (99.2%), heritability estimate for maximal muscular power as determined from the measurement of the maximal running velocity on a staircase and the subjects weight. However, no attempt has been made to derive heritability estimates for maximal muscular power based upon individual force-velocity curves.

Therefore, the problem of this investigation will be to ascertain to what extent heredity contributes to inter-individual variation in the force-velocity relation of human muscle. More specifically, the twin study method of research will be employed for the purpose of attempting to derive heritability estimates for the following components of force-velocity curves obtained from the forearm flexor muscles. The components to be studied are:

(1) the maximal muscular power developed by the forearm flexor muscles as derived from individual force-velocity curves;

(2) the maximal velocity of movement (V_{max}) of the forearm produced by the contracting forearm flexors under unloaded conditions; and

(3) the maximal isometric force (P_o) produced by the forearm flexor muscles at an elbow angle of 80 degrees.

Limitations of the Study

(1) Errors in calibration, testing precision and standardization;

(2) Errors in drawing the "best fit" force-velocity curve from the experimentally obtained values;

(3) Degree of repeatability of the test;

(4) The shout method will be used for motivation.

Delimitations of the Study

(1) The study will be delimited to a sample of nine sets of monozygotic twins and eight sets of dizygotic twins. Their ages range from 11 to 17 years.

(2) Only two measurements will be obtained for maximal isometric force (P_o) for the forearm flexor muscles and will be analyzed at one elbow angle (80 degrees). The highest value will be used.

(3) Only two measurements will be obtained for the maximal velocity of movement (V_{max}) of the forearm under unloaded conditions and will be analyzed through a range of 50 degrees. The highest value will be used.

(4) Only one single maximal voluntary contraction of the forearm flexor muscles will be obtained for one load. As many different loads as possible will be used in order to obtain as many force-velocity values that will increase the accuracy of the drawing of the curve.

(5) All force-velocity values obtained from the different loads will be analyzed through an elbow range of 50 degrees. The highest values will be used.

(6) The maximal muscular power curves will be obtained from the "best fit" force-velocity curves.

Theoretical Framework for the Investigation

When the twin study method was proposed by Galton, the distinction between monozygotic (MZ) and dizygotic (DZ) twins was not clearly understood (21). It is now known, that MZ twins have resulted from the cleavage of a single zygote into two separate embryos. Because of the precise nature of mitosis and DNA replication, MZ co-twin pairs have received identical genetic constitutions. Most commonly, the individual embryos have individual amnions with only one chorion and a single placenta. However, it has occurred that MZ twins have two amnions, two chorions and two placenta (although often fused) (3,5,14,64).

Dizygotic twins have resulted from the separate fertilization by two different sperms of two ova released from the same or more often, different follicles at about the same time. Since DZ twins arise from two zygotes that are produced by fertilization of two separate ova, they have the same genetic relationship as ordinary siblings and differ approximately 50% in their genetic constitution (3,5, 14,64).

The twin study method has compared the degree of divergence (or lack of concordance) between a sufficient number of MZ and DZ co-twin pairs of the same sex, in order to estimate the extent to which variation in heredity has accounted for the individual variation in any organic attribute. Since DZ twin pairs differed approximately 50% in their genetic make up, while MZ twin pairs are identical, any performance difference between MZ co-twin pairs must have been due to nongenetic factors. As stated previously, in order for any comparison to be made between MZ and DZ twins in the twin study method, two basic assumptions must be accepted. Firstly, that the amount of within pair variance contributed by the pre and postnatal environmental influence for MZ twins, is comparable to that for DZ twins and secondly, that no heredity environment interaction is present (47,59,61,84).

Considering the first assumption, it has been understood that a difference in prenatal environment for the MZ twins (unequal circulation, nutrition, intra-uterine position), may possibly produce postnatal structural and biochemical differences. Further, experimentation has revealed that modification of cellular cytoplasmic agents has induced postnatal differences (8,10,19,23,24,38,62). In as much as these prenatal differences may exist for some MZ twins, it is presumed that any unequality suffered during the prenatal period is not enduring, and is neutralized after birth under the influence of a genetic maturational pacemaker (46,56). The twins that were temporarily grouped as monozygotic in this study, using the "physical similarity" method of classification (61), revealed no such structural abnormalities or differences.

Regarding the tenability of the assumption of comparable postnatal environmental influences for MZ and DZ twins, it is obvious that, the more similar the population from which the twins are drawn, the less likely are discrepant results. All co-twins employed in this study were obtained from the same city, lived at home with their parents and had similar leisure-time activities and socioeconomic backgrounds. The assumption of similar postnatal environments for MZ and DZ twins does not imply "invariant environments", but that the environment "varied approximately in the same direction and to the same degree" for all twins in the study (56). Vandenberg (77), has suggested that for psycho-motor functions, and for cognitive abilities, one could envisage some division of labor or specialization occuring within a twin-pair such that one twin developed more in one direction. However, this may occur in MZ as well as DZ twins, and even if it happened more in DZ twins, it may be attributable to a greater initial divergence resulting from hereditary differences. If environmental influences within the family were in part responsible for greater differences in, for example, cognitive abilities within DZ twin-pairs than within MZ twin-pairs, it may be expected that the correlations between the differences of twins on a variety of tests appeared quite high. Vandenberg (77) has pointed out however, that this is not the case. Jensen (37) has also indicated that the assumption of greater environmental differences for DZ than for MZ twins has not been established as a fact (31).

There have been some attempts to obtain evidence on the validity of the assumption of equal differences on the average between MZ and DZ twin partners due to the degree of familial influence (40,58,63,86). All these studies postulated increased pressure toward similarity and a greater intimacy in MZ twins, but, "they attempted to support this hypothesis by an analysis of measures obtained retrospectively on the twins; the extent to which the evidence thus obtained is relevant, may be questioned" (77). On the other hand, even when reared apart, MZ twins have shown important mental and behavioral similarities (39,71).

For physiological variables however, "be they of central nervous system or of autonomic nervous functioning, it is still difficult to question the assumption seriously" (77). In view of the evidence, it appears justified to accept the assumption of comparable postnatal environmental influences between MZ and DZ twins.

The second assumption is that no genetic-environmental interaction is present. Put in other words, that for the total variance for MZ and DZ twins respectively, "hereditary and environmental components have zero correlation" (61) In order that the magnitude of interaction effects be ascertained for any specific trait, "empirical study" is necessary (37). In this respect, limited data are available as to whether different genotypes respond in different ways to the same environmental factors. For physiological variables, this has required the utilization of split-twin experiments, in which one twin trained for a specific variable in question while his identical counterpart acted as a control. Recent data obtained from split-twin training experiments on $\dot{V}O_2$ max have revealed that for this variable, the interaction between heredity and environment was a nonsignificant cause of the total variance (83). Whether the same conclusion can be drawn for the specific neuromuscular variables that will be investigated in this study, it seems that no tenable conclusions can be drawn at this time. The simple additive model of heredity plus environment to be presented may not be adequate to explain to the observed within-pair variance of DZ twins and it should be modified to include an additional term signifying the mutual interaction between heredity and environment. However, it is unlikely that such interaction took place to any marked degree in the present subjects. Most of the twins will be at an early age of development and the differences in environmental influence will not be as pronounced at this period as they would be at the later developmental stage (47). Rigorous evidence of heredity-environment interaction is needed for the specific variables under study before this component need be included in the heredity-environment model. Therefore, it seems "justifiable to omit this component from the computations of heritability estimates without risk of serious error" (47).

In order to make the assumptions behind the computation of heritability estimates more explicit, a simple additive model for the effects of heredity and environment has been postulated. The model has taken into account the preceding assumptions of comparable pre and postnatal environmental influences for MZ and DZ twins and nil heredity-environment interaction. For MZ twins, since there is no genetic variability, the within-pair variance (W^2) is attributed to nongenetic variability, namely environmental effects (W^2_e) and measurement error (W^2_m):

$$W^2MZ = W^2MZ_e + W^2MZ_m \qquad \text{(III)}$$

For DZ twins, the within-pair variance depends partly on genetic variability (W^2_g), partly on environmental effects (W^2_e) and partly on measurement error (W^2_m):

$$W^2DZ = W^2DZ_g + W^2DZ_e + W^2DZ_m \qquad (IV)$$

If the comparable environmental influences are excluded and equations III and IV combined, the within-pair variance in DZ twins due to variation in heredity can be denoted as.

$$W^2DZ_g = (W^2DZ - W^2DZ_m) - (W^2MZ - W^2MZ_m) \qquad (V)$$

Further, if equation V is arranged in ratio form, and the term W^2DZ_g referred to as heritability estimate (H_{est}) (4,47,77), we have (47):

$$H_{est} = \frac{W^2DZ - W^2MZ}{W^2DZ - W^2DZ_m} \times 100 \qquad (VI)$$

Thus, the heritability estimate is the ratio of the difference of the within-pair variances between DZ and MZ twins, to the total within-pair variance among DZ twins. Equation VI is only introduced when the F-ratio, as proposed by Clark (7), is proved significant at the required level of confidence. The F-ratio is between the DZ and MZ within-pair variances and is written as:

$$F = \frac{W^2DZ}{W^2MZ} \qquad (VII)$$

If the F-ratio proved significant at the required level of confidence, heritability estimates are derived from equations I or VI. It should be emphasized that the heritability estimates so derived do not indicate to what extent a trait is inherited, but only to what extent its variability was governed by variation in heredity (60).

The confidence placed in any conclusions drawn from the twin-study method of research depends on the accuracy with which the twins were classified as MZ or DZ. With the possible exception of a successful skin graft or reliable evidence of a single chorion, no similarity in a single trait has so far been shown to be sufficient on its own to prove that a pair of twins is monozygotic (61). Consequently, the onus is placed on utilizing methods to establish dizygosity. This is achieved by the "physical similarity method of classification " (71). This method groups the twins as alike or different in a number of morphological traits that are known to be highly determined by heredity (7,76). Monozygotic twins have similar hair color, texture and distribution, similar ear lobes, eye color and iris pattern. In addition, careful attention is noted as to the similarities and differences in the height and weight, the shape of the facial features, the teeth and the size and shape of the hands. In this way, a preliminary rough diagnosis is made prior to any testing session. However, the most reliable objective test for zygosity is to have a blood and serum examination performed on all subjects after the results are obtained and analyzed. A sample of blood is taken by finger prick and is analyzed for red cell antigens with numerous Anti-sera. Discordance of a single antigen is regarded as evidence of dizygosity (42). In this manner, exact diagnosis is made in about 98% of all DZ pairs (76).

The value of twin studies depends not only on an accurate diagnosis of zygosity but also on an accurate assessment of the relative exposure to environmental influences that are most likely to affect the magnitude of the differences in the variables under study. Therefore, twin studies make a careful assessment of these environmental influences before postnatal environments can be assumed to be comparable between MZ and DZ twins.

CHAPTER II

REVIEW OF THE LITERATURE

The literature relating to the force-velocity relationship has been reviewed under two headings: (1) isolated striated muscle and (2) intact human muscle. In some instances, reference is made from one area to another because both have contributed to the development of the force-velocity relationship as it is understood today.

The literature relating to twin studies is reviewed under two headings: (1) cardiovascular variables and (2) neuromuscular variables.

The Force-Velocity Relationship

(1) Isolated Striated Muscle

In 1920, Hill (29), described a useful inertia device as an instrument for recording the maximum work done in a frog muscle during muscular contraction. The recording system suggested by Hill and employed and described fully by Doi (12), consisted of an arm balanced on knife edges carrying two balanced masses. The rate at which the muscular contraction occurred could be varied by changing the point of attachment of the muscle or the distance of the balanced masses of the system.

Gasser and Hill (22) used a double sartorius preparation of the frog to show the relation between the speed of shortening to its ability to perform external work. The muscles were allowed to attain their maximum in an isometric tetanus before being released and were then allowed to shorten between two fixed points. An effect was obtained equivalent to allowing the muscle to pull against a wide range of freely suspended masses. The results indicated that the work performed decreased as the speed of shortening increased. However, the curves relating work to speed of shortening were not linear.

Gasser and Hill (22), then used two methods to show the effects of the speed of shortening of the muscle to the force developed. In both methods, the rate at which the muscle shortened was controlled. They concluded that the greater the speed of contraction, the less the force exerted at any length. Gasser and Hill explained their results in these words, "the dependence of force exerted on the speed of shortening was the result merely of the viscosity of the muscle".

Levin and Wyman (53), obtained the work done by the jaw muscles of the dogfish by measuring the areas of the tension-length curve. The work was plotted against the speed of movement for quick release and stretch experiments. The resulting curves were not linear but S-shaped, and to Levin and Wyman, this suggested the presence in the muscle of an element of free or undamped elasticity.

Hartree and Hill (26) utilized the identical method to determine work as Levin and Wyman (53). Results indicated that if the shortening speed was too high or too low, little work was done. For the high speeds of contraction, Hartree and Hill believed that little work was done because of the viscosity of the muscle, which increased with the rate of shortening.

Stevens and Snodgrass (74) used the gastrocnemius muscle of the decerebrate cat to determine the speed of shortening of the muscle, the force developed, the work done and the power expended during each 0.011 second of the contraction cycle. With the method employed, both the tension and length of the muscle were allowed to vary concomitantly during the same contraction against an inertia system. It was thus possible to determine accurately the entire range of tension and corresponding length changes throughout the same contraction cycle. The results presented were the averages of eleven records obtained from the same animal during the same experiment. They were selected as representative of a series in which twenty animals were used. The curve relating the force developed to the velocity of muscle shortening revealed that as the speed of contraction increased, once the muscle had developed maximal tension, the force diminished. They concluded that some of the loss of force was due to the viscosity of the muscle. Further, that the inverse relationship between velocity of contraction and force depended upon the fact that constant power was exerted by the muscle at this time.

Stevens and Metcalf (73) used the same apparatus and method as that used by Stevens and Snodgrass (74). The velocity of the muscle, force, work and power were calculated for small time intervals of the contraction cycle. Results were chosen from one cat as typical of the fifteen animals used in the series of experiments. All experiments were quick releases which meant that the muscle was prevented from moving until the muscle had contracted tetanically. When the force was plotted against the corresponding speeds of shortening, they concluded that over a certain portion of any given contraction the force varied in a linear manner with increasing speeds of shortening. The results were interpreted and explained by the viscous-elastic theory as proposed by Hill (30), that the decrease in force might be predicted "with certain simple assumptions as to the viscous resistance of the muscle to change of form".

Fenn and Marsh (17), used the sartorius muscle of Rana pipiens except for a few experiments on the gastrocnemius to show the relationship between the force exerted by the muscle and its velocity of contraction. The velocity of contraction was always measured near the beginning of shortening where the slope was constant and maximal. No attempt was made to calculate the magnitude of inertia. It was reasoned, that since there was no change in velocity, the tension in the muscle would be equal to the load. The force was calculated per cm^2 cross section of the muscle. In most experiments, the muscle was stimulated for a series of loads increasing in steps from minimum to maximum and then decreasing in the reverse order. Therefore, Fenn and Marsh measured the maximum speed of shortening under a series of different loads, the measurement being made always at approximately the same muscle length. When the force or load was plotted against the velocity of shortening, the investigators concluded that the curve was not linear, but rather logarithmic in shape. They further concluded that as the speed of shortening increased, the force decreased, not in a linear fashion as would be expected if viscosity alone was concerned, but rather in an exponential fashion, a small hypothetical correction being made for the true viscosity effect. Fenn stated that "this exponential relation was concerned in some way with the processes of developing extra energy for work of shortening".

Hill (28) developed a more exact and rapid technique for muscle heat measurements so that a more consistent picture might emerge of the energy relations of muscle shortening (or lengthening) and doing positive (or negative work). Hill showed that if a frog sartorius muscle, mounted on a thermopile, was stimulated isometrically and then suddenly released under a small load, it shortened rapidly and during the shortening the galvanometer gave a quick extra deflection. To Hill, the extra deflection implied a sudden increase in the rate of heat production of the muscle. Hill postulated that when a muscle shortened, extra heat was liberated. Experimentally, Hill found that the rate of extra energy liberation was a rather exact linear function of the load, increasing as the load diminished and being zero when the load was equal to the maximal isometric force. Hill put forth an equation which related the rate of energy liberation to the load. The equation was:

$$(P + a)v = b(P_0 - P) \qquad \text{(VIII)}$$

where,

P = the load on the muscle;

a = a constant with the dimension of force;

v = the velocity of shortening;

b = a constant defining the absolute rate of energy liberation; and

P_0 = the maximal isometric force.

This equation was also written as:

$$(P + a)(v + b) = (P_0 + a)b \qquad \text{(IX)}$$

which related the velocity of contraction and the force in isotonic shortening. In this equation;

P = the load on the muscle;

a = a constant with the dimensionof force;

v = the velocity of contraction;

b = a constant with the dimension of velocity; and

P_0 = the maximal isometric force.

In another set of experiments, Hill (28) showed that when a contracting muscle was made to lengthen gradually by applying a load rather greater than isometric tension, there appeared to be a negative heat of lengthening and the total energy given out by the muscle was less than in an isometric contraction. These experiments on heat and lengthening made it impossible any longer for Hill to regard viscosity as the primary cause of the effects observed in active muscle. He stated, "if viscosity were the chief reason for a decrease in force as the velocity of contraction increased, then lengthening of the muscle should produce greater heat production and certainly not less than isometric tension".

In a number of other experiments, Hill (28) used a series of different loads with the constants a and b previously determined to show the relation between the speed of shortening and load in an isotonic contraction. Hill found that the experimental points of load and velocity fit the curve described by his "characteristic equation". He concluded that an active muscle shortened more slowly under a greater force, not because of viscosity, but as Fenn (17) had claimed, "to the manner in which the energy liberation was regulated". Further, Hill deduced from the force-velocity curves, that the greatest rate of doing external work (power), should occur with a load equal to about 30% of the isometric tension.

In continuation of Hill's work, Katz (44), performed experiments to confirm the force-velocity relation utilizing Hill's characteristic equation. The experiments were made on the sartorious muscle of Rana temporaria, Rana esulenta, and on the retractor penis of the tortoise. The muscle was extended by a small initial load and allowed to shorten several millimeters against various loads. Katz tested the predicted relation of the force-velocity curve using the values of the constants a and b from Hill's equation. In most cases, the observed experimental data fitted the rectangular hyperbola predicted by the equation which related the velocity of shortening and the external force.

Abbot and Wilkie (2), described experiments in order to examine the relation between force and velocity in lengths other than that which was found in the resting condition in the body. The reason was that Hill's equation could only be applied in the region of this maximum, where the variation of maximal isometric force with the length of the muscle was slight; for the maximal isometric force appeared in the equation as a constant. All experiments were made on the sartorius muscle of Rana temporaria. Tension-length curves were measured before and after the series of isotonic shortenings. Conclusions drawn from the results, showed that Hill's equation did apply at all degrees of shortening as long as the isometric force at any length at which the velocity was measured was given the new value appropriate to that length.

MacPherson (55) compared two isometric contractions, one with and the other without a known compliance added in series, in order to calculate the force-velocity relation of the frog sartorius muscle. The sole assumption required was that the velocity of shortening at any moment was a function only of the load at that moment. The tension developed by the muscle and the rate of change of tension were recorded simultaneously throughout the growth of a maintained isometric contraction. A similar record was made with extra compliance. The results revealed that the force-velocity curve always emerged with the expected hyperbolic form.

Ritchie and Wilkie (66) used the sartorius muscle of the frog to determine force-velocity curves from after-loaded isotonic contractions. They found that about one-third of the force-velocity curves from the experiments were not fitted well by Hill's equation because they had a straight region at the high force - low velocity end. Ritchie and Wilkie found a somewhat better agreement between experimental results and the predicted curve by using Carlson's equation which was not tied down to any specific algebraic formula for the force-velocity curve.

Hill (27) used the frog sartorii muscles to show the efficiency of mechanical power development and its relation to load. In most of the experiments the muscles were allowed to shorten as soon as they could lift the load. In a few, they were released later. Hill compared the load with which the mechanical power was greatest with that at which the efficiency was greatest. Hill found that the optimum load for efficiency was about 45% full isometric tension. The optimum value for power development was practically constant at about 30% of maximal isometric force

(2) Intact Human Muscle

Hill (30) devised a heavy fly-wheel to provide the inertia against which the arm muscles had to work. A string was attached around one of the pulleys and the subject pulled the end of the string which produced rotation of the flywheel. Variation of the equivalent mass of the flywheel was obtained by winding the string around one or the other of the different sized pulleys of the flywheel. The speed of rotation was measured by a hand tachometer. In all subjects tested, the results clearly indicated that the greater the equivalent mass, the greater the work done. Hill also found that the greater the duration of shortening, the greater was the work done. Hill hypothesized that a muscle, when stimulated, produced potential energy which in any actual contraction was employed partly in doing external work, and partly in overcoming the viscous resistance of the muscle to its change of form. Further, the energy dissipated in overcoming the viscous resistance to a given change was proportional to the speed with which the change was carried out and to the coefficient of viscosity of the muscle fluids.

Lupton (54) re-investigated Hill's findings with certain modifications of the method utilized. A "quick release" mechanism was designed to insure that the movement did not commence before the maximum force of the muscle had been developed. The speed of rotation was measured by a hand tachometer. As Hill had done, Lupton eliminated errors due to fatigue by having the starting point of the experiments the pulley with the largest equivalent mass, taking readings on each pulley until the one with the smallest equivalent mass was reached and then repeating in reverse order. Lupton's results were in agreement with those of Hill, that the external work was diminished through viscosity by an amount depending upon the velocity of shortening.

Hansen and Lindhard (25) used an apparatus similar to Hill's heavy fly-wheel. The work actually performed in a pull was determined for a series of pulls by the same subject. Two series were performed on the same day, firstly, a series beginning with the greatest pulley and ending with the smallest and later, a series in the reverse order. The duration of the pull was determined by means of a stop watch. Tension was determined by inserting a Collins dynamometer between the handle of the string and the inertia wheel. The subject placed his arm on a table and while the length of the string was successively varied, made a series of maximal pulls against the dynamometer. In this way, the angle of flexion of the elbow joint corresponding to a point where maximal tension was exerted could be constructed graphically. Results regarding the relation between work and varying the equivalent mass were quite similar to those obtained by Hill (30). However, their results indicated that the coefficient of viscosity was not a constant but a variable which included a constant viscosity factor.

Hill, Long, and Lupton (32), chose a given pulley of the inertia wheel and had the subject make a series of maximal contractions employing the quick release mechanism On a signal, the subject made and maintained a maximal effort and after an interval measured on a stop watch, the wheel was released. The interval was varied arbitrarily between 0 and 3 seconds, the subject having no idea what it would be in any given contraction. Plotting the work against the duration of the isometric interval, they concluded that a 6% reduction in work was a good mean estimate for the effect of each second duration on the work of previous maximal contractions. Further, the work decreased in a linear manner as the speed of shortening was increased.

On the assumption that the force exerted by a runner was used mainly in overcoming the viscosity of his own muscles, Furusawa, Hill and Parkinson (20) developed an equation to show that the motion of a runner, starting from rest and exerting a maximal effort, propelled himself with a constant force which was retarded by a resistance proportional to his speed.

Best and Partridge (6) used the equation of the motion of a runner, to investigate whether the maximum speed obtained by a runner depended upon the maximal force and the frictional resistance of the muscles. One subject was used to study the effects of external resistance because this subject could reproduce his maximum speed in different runs on the same day with great consistency. As a routine procedure, the subject first ran without an external resistance, then two or three runs with different external resistances and a final run without resistance. The results showed that the average difference between the observed maximum speeds and that calculated from the equation was approximately 0.015 yds. per second. Therefore, the maximum speed of the subject when external resistance was applied was decreased by an amount calculated from the equation of a runner. They concluded that the internal resistance of the muscles (viscosity) was real in a sense that it had identically the same effect as an externally added resistance.

Dickenson (11) described an investigation to determine the maximum speed of pedalling a bicycle ergometer as a function of the load applied to the wheel. In each recording the subject began with one pedal ready to be pushed downwards at an angle of 45° from the top position. The subject pedalled as fast as possible for about ten seconds. The maximum speed was found to be attained about four seconds from the start. The results indicated that the relation between maximum speed and load was linear.

Fenn (16) illustrated a new method of demonstrating muscle viscosity in sprint running. The subject sat on a table with one leg hanging over the edge and arrangements were made for recording variations in the angle of the knee with time as the lower leg moved. A curve was traced by a pointer on a revolving drum as the lower leg moved which indicated angle of the knee plotted against time. The slope of the curve represented the angular velocity. If the angular velocity measurements were plotted as a function of time, the slope of the resulting graph presented the angular acceleration. The results indicated how quickly the force decreased following a quick release of the lower leg. Fenn suggested that the failure to develop force while shortening may be due partly to a reflex cessation of stimulation or a reflex inhibition. He also suggested that the loss of force may be due to some characteristic of the muscle itself. He stated that "the delay in development of tension might equally well be in some chemical reaction involving the mobilization of the necessary energy for contraction. In such a case, the term viscosity would be inappropriate".

Fenn, Brody and Petrilli (18) made arrangements to obtain a kymographic record of the position of a moving arm or leg as a function of time. The slope of this graph gave the angular velocity at every moment during the movement. If these velocities were plotted, a smooth graph drawn through the points, the slope of this curve gave the angular acceleration of the movement. Knowing the moment of inertia of the limb, the force exerted at various moments could be calculated. The force exerted by the subject was determined at the moment when the limb was held isometrically and then suddenly released by pulling a pin. From the resulting acceleration of the limb as deduced from the graphical record of the swing, the moment of inertia of the limb was calculated and was found to agree within 10% with the value estimated from the weight of the individual and the dimensions of the limb. When the force exerted in the "quick release" experiment was plotted against the velocity at different moments during the swing, it was found that the tension decreased as the speed of movement increased. The average rate of decrease of muscle tension so determined was 3.1% for a rate of shortening of 10% of the muscle. It was concluded that 3% represented a maximum figure for the effect of viscosity alone.

Dern, Levene, and Blair (9) studied the relationship of force to velocity in maximal flexions of the human forearm. The apparatus was designed to supply constant force with as little inertia in the system as possible. The force could be used directly or converted to a constant torque to oppose the movement of the arm. In order to produce a series of moments of inertia about the elbow joint, flat lead weights of 1 Kg. mass were added to the end of a lever. The movement in all experiments was recorded when a thread from the periphery of a small pulley was attached to a lever which wrote on a kymograph. Therefore, the instantaneous velocities at a series of points along the contraction could be determined. The subject made a maximum voluntary flexion against opposing loads applied in three ways: (1) the reaction of various moments of inertia; (2) constant torques about the elbow joint; and (3) isotonic forces applied parallel to the forearm flexor muscles. The results revealed that the force-velocity curves obtained at 80% of flexion for contraction against inertias and constant torques were similar for a given subject but were different from the curves with techniques using increasing torques. The experimentors concluded that force-velocity curves were different when different techniques of applying the opposing loads were used. Further, since electromyography records indicated activity of antagonist muscles in all contractions, they believed that the true force-velocity curve of human muscle must lie outside their experimental curves; the true isometric force would be greater than that measured at 80° flexion and the maximum velocity in the order of 160% of the measured maximum. They stated that "the exact course of the curve is not determinable from simple force-velocity measurements in the intact arm". Although the data could be rather accurately represented by a rectangular hyperbola, they concluded that there was no evidence that the characteristic equation developed by Hill (28) would be applicable to human isolated muscle.

Ralston, Polissar, Inman, Close and Feinstein (65) studied voluntary contractions of the human pectoralis major, biceps brachii and triceps muscle under isometric and isotonic conditions, in subjects having cineplastic muscle tunnels. The isometric contractions were measured with a strain gauge dynamometer. For the measurements of rates of shortening of the muscle under various loads, a light lever constituting one arm of a resistance bridge, was connected to a cable supporting the load. As the load was lifted, the bridge unbalance was measured by a Heiland type A galvanometer and recorded on a Heiland type SE-301 R-12 oscillograph. Concerning the relation between load and maximal velocity, every attempt was made to reproduce as closely as possible the experiments made on a frog and cat muscle by Fenn and Marsh (17) and on frog muscle by Hill (28). The muscle was initially stretched with a load of 0.32 kg. to a length slightly beyond resting length, all greater loads being supported by a block. The subject was instructed to shorten his muscle as rapidly as possible upon receiving a signal. At least two sets of measurements, in ascending and descending series, were made in each experiment. The maximal force which the muscle could develop at the initial length was determined with the isometric dynamometer. The results indicated that the curve relating load and maximal velocity could be fitted by the characteristic equation, as found by Hill (28) for frog muscle.

They further concluded that an isolated human muscle would develop maximal power when lifting a load equal to about one quarter to two fifths of the maximal isometric tension the muscle can develop.

Wilkie (85) used an apparatus which consisted of a triangular oak lever axle which ran freely in self-centering ball bearings which were mounted on blocks at the end of a table to determine the relation between force and velocity in human arm movement (70). The subjects pulled on a lever through a Bowden wire cable in which the tension was varied by altering a suspended weight. The subject kept his upper arm fixed during each movement by pressing it up against a padded block of wood fastened to the table. Movement of his body was prevented by a vertical board at the end of the table. In order that the force applied by the arm be constant throughout each movement , the cable must remain horizontal. The velocity of each movement was estimated from a charge which accumulated on a condenser. The velocity of the subjects' hand was always measured at the end of the movement, when the arm was at an angle of 80° with the horizontal. The load was supported by a stop so that the lever was at 40 degrees with the horizontal before each movement. At the end of the movement (75°) the load was held by a spring catch. The isometric tension was measured by a simple spring balance, with the forearm at an angle of 80 degrees with the horizontal, that is, in the same position at which velocity was measured. For one subject, the tension at the hand was varied in eleven steps from 0-15.23 megadynes and at each step 30 measurements of velocity were made. Only five velocity measurements at the same tension were made at one time and each one followed a rest period of at least one minute to avoid fatigue. When the experimental relationship of mean velocity was plotted against the force it remained to be seen whether the experimental exponential curve would be described by Hill's characteristic equation. After a few trials, it became clear to Wilkie that the experimental results did not fit the equation except at tensions greater than .3 P_0. It seemed to Wilkie that the inertia of the apparatus and forearm might so diminish acceleration that the full velocity could not be reached before the movement was completed. After correction for the inertia of the forearm and the apparatus, the force-velocity curve could be represented by Hill's equation (28). Experiments were done on another 4 subjects and each experimental point of the force-velocity curve was based on 5 instead of 30 determinations of velocity. The fit with the characteristic Hill equation was in every case quite good. Although the maximal force varied in subjects from 12 to 20.5 megadynes, the maximal velocity of movement attained was relatively constant (670-775 cm/sec), a finding reported previously be Dern _et al_. (9).

Komi (49) presented a report which dealt with a dynamometer designed for the measurement of the force-velocity relationship of the human forearm flexors and extensors.

The dynamometer was capable of recording both the isotonic force (either eccentric or concentric) and changes in muscle length (elbow angle) with 8 different velocities of shortening and lengthening of the elbow flexors and extensors. Thus, to obtain the force-velocity relationship, a total of 16 different constant speeds could be selected along with the velocity axis. The dynamometer was so constructed that the velocity of lengthening and shortening of the biceps brachii muscle remained as constant as possible throughout the movement range of approximately 120°. This corresponded to a 7 cm. change in length of the biceps muscle of an adult man. The speed range varied from 0.8 to 6.7 cm. per second when measured from the biceps muscle. The velocity of contraction was obtained with a photo-electric transducer which gave an impulse on an oscillograph at each spindle revolution. Strain gauges to record the force were installed on both sides of a special wrist cuff, which allowed the wrist to be fixed at any desired position between full supination and full pronation. The force-velocity curves that were obtained for the elbow flexor muscles followed closely the classical force-velocity relationships obtained with isolated muscle.

Ikai (35) has tried to approach the problem of training of muscular power by considering the force-velocity curve of muscle. He measured individual force-velocity curves of the forearm flexor muscles for thirteen male and fifteen female adults. The maximum power was calculated to be found when the force and velocity were about 35% of the maximum values in both sexes. A power training study was conducted in twelve male adults to see the effect on the force-velocity relationship of the forearm flexor muscles. The load used for training was zero, thirty, sixty, or one hundred percent of the maximum isometric strength. The training consisted of ten maximal voluntary contractions of the elbow flexors once a day lifting the load specific to the group. The results indicated that a greater displacement of the force-velocity curve, and consequently better all-around improvement in maximal muscular power, was obtained with the subjects that used the thirty and sixty percent training loads. He concluded that for all-round power training, that a load from thirty to sixty percent of the maximum strength should be used.

Summary

Because the review of the literature on the force-velocity relationship of contracting muscle is quite extensive, a brief summary is presented in order that a general picture may be obtained of its development and importance.

The discovery of the force-velocity relation really began with preliminary studies that were concerned exclusively with the relation between the speed of muscular contraction and the external work. It was shown that for the isolated striated muscle (22,26,53), as well as the intact human muscle (25,30,32,54), that the work decreased as the speed of shortening increased. Hill (30) fostered the belief in his early work on human arm movements, that the potential energy for contraction was used partly to overcome the viscous resistance of the muscle to its change of form and that the energy used was proportional to the speed of shortening. All the early studies which related speed of shortening to work (22,25,26,30,32,53,54), and some which related speed to the force exerted (6,73,74) have postulated that viscosity was responsible for the inverse relationship which was found. A discrepancy arose in these early studies as to whether the relationship between speed and work or speed and force was linear or not. Some studies (11,30,32,54) concluded a linear relationship, while others (22,26,53) did not.

The dilemma continued until the work by Fenn (16) on intact human muscle, suggested that the loss of force may be due to a characteristic of the muscle itself rather than viscosity. Subsequent work by Fenn and Marsh (17) concluded that the relationship between force and velocity was not linear as would be expected if viscosity alone was responsible. This was re-affirmed by Hill (28) with his experiments on heat and lengthening. In the same experiments, Hill (28) proposed his force-velocity equation which related the velocity of contraction and the force in an isotonic shortening. Investigations have confirmed, that experimental data can be fitted to the rectangular hyperbola predicted from Hill's equation for isolated striated muscle (2,44,66), as well as the intact human muscle (65,85). For isolated striated muscle, it has been found that the force-velocity relationship holds true for muscle lengths other than that found in the resting condition of the body (2), can be measured by comparing two isometric contractions (55) and can be predicted from other equations (66). For intact human muscle, it has been found that the force-velocity relationship can be different for different techniques of applying the loads (9) can be fitted by Hill's equation in subjects having cineplastic tunnels (65), can be measured for flexor or extensor muscles (49), and can be displaced by training (35). Further, for both types of muscle, it has been shown (27,35) that maximal muscular power is developed when the load on the muscle and its velocity of contraction are approximately one-third of their maximum values.

Twin Studies

Much of the literature relating to the twin method of research has been presented under the theoretical framework for the present investigation. It is recognized that a great amount of twin research has been attempted for psychological measures (perceptual tasks, cognitive measures, personality). However, to review all studies in this area is beyond the scope or the intention of the present investigation. Therefore, only investigations that have used twins to study physiological variables have been reviewed. The review is divided into two headings: (1) cardiorespiratory variables, and (2) neuromuscular responses.

(1) Cardiorespiratory Variables

Kryshova (51) has reported a high concordance for MZ twins on changes in blood pressure due to hot and cold stimuli. In addition, each MZ twin pair showed concordance in the number of stimuli required for adaptation.

Vandenberg, Clark, and Samuels (82), found evidence of hereditary components in the reactions to mild stress by changes in heartbeat frequency and breathing rate.

Klissouras (47) found the intra-pair difference in maximal oxygen uptake was greater between DZ than MZ twins. The heritability estimate revealed that the variability in maximal oxygen uptake was genetically determined by 93.4%.

Arkinstall et al.(4) found that the intra-pair difference in the tidal volume response to CO_2 stimulus expressed as a ratio of the vital capacity was significantly greater between DZ than MZ twins. The heritability estimate was 80-90%.

Finally, as cited by Klissouras (47) a strong hereditary component has been reported for lung volumes, maximal heart rate, QRS and QT intervals of the resting electrocardiogram.

(2) Neuromuscular Variables

Lennox, Gibbs, and Gibbs (52) have shown a hereditary component in the brain wave pattern as measured by an EEG.

Jost and Sontag (41) compared galvanic skin response records of siblings and a few pairs of MZ twins and concluded that there was evidence for an hereditary factor.

Vandenberg (80) and Sank (68) have both reported that standard audiometric techniques with twins give evidence of some hereditary component within the normal range of performance

Eysenck and Prell (15) have reported some indication of an hereditary component in the critical fusion frequency for a flickering light. Further, they revealed hereditary components in tapping speed. This motor skill test was reported by Newman, Freeman and Holzinger (59) and they also found hereditary components were involved. Other motor skill tests of pursuit rotor hand steadiness by McNemar (57) and card sorting by Vandenberg (78) have shown hereditary factors.

Komi, Klissouras, and Karvinen (50) measured reflex and reaction time and nerve conduction velocity in the ulnar nerve and found marked differences between MZ and DZ twins. The heritability estimate was high for reflex and reaction time but low for nerve conduction velocity (97.5 and 85.7%, respectively). In the same study, Komi used 29 pairs of twins (15 MZ and 14 DZ) of both sexes to ascertain the heritability of maximal muscular power. They computed power output on the basis of the subjects' body weight and the maximal running velocity on a staircase. Komi reported a heritability estimate for maximal muscular power of 99.2%. However, a statistically significant variation between MZ and DZ twins was not observed in mechanical power output expressed in Kpm/KgBW/sec or in maximal running velocity. This implied to the investigators that "the variance in maximal muscular power may not be due to an individual difference in the splitting rate of high energy phosphate compounds, but to a quantum, that is, to a greater amount of adenosinetriphosphate and phosphocreatine which are made available as a result of a greater mass of protoplasmic tissue".

CHAPTER III

METHODS AND PROCEDURES

Subjects

Male monozygotic twins (N=9 pairs), and like-sexed dizygotic twins (N=8 pairs), were used as subjects in the present investigation. The male twins were obtained from greater metropolitan Montreal and lived at home with their parents. The twins ranged in age from 11 to 17 years.

Anthropometrical Data

The following anthropometrical data was collected from each twin: age (years); height (cm.); and weight (Kg.)

Zygosity

A preliminary rough diagnosis was made by the similarity method of classification. The method groups the twins as alike or different in a number of morphological traits that are known to be highly determined by heredity (7,76). The subjective criteria that were used are presented in Appendix A.

A blood and serum examination was performed on all twins after the results were obtained and analyzed. A sample of blood was taken by finger prick at the home of the twins and analyzed in the laboratory for red cell antigens with the following anti-sera: Anti-A; Anti-B; Anti-AB; Anti-Le^a; Anti-Fy^a; Anti-C; Anti-D; Anti-K; Anti-k; Anti-M; Anti-N; Anti-s; and Anti-Human. The method followed for the blood grouping was based on information supplied with the DADE Anti-sera. Discordance of a single antigen was regarded as evidence of dizygosity (42). In this manner, exact diagnosis was made in approximately 98% of all DZ pairs (76).

The Ergometer

An ergometer was specifically designed to permit determination of the force-velocity relationship of the forearm flexor muscles as they collectively exerted their force at the palm of the hand. The ergometer was constructed in such a way that minor adjustments allowed the right or left arm to be tested. The subject was seated and placed his dominant upper arm on a rest at a right angle to his upper body and in line with his shoulders. Adjusting the height of the arm rest or the seat, maintained this position. Further, the elbow joint was maintained directly in line with the pivot axis of the lever arm of the ergometer by adjusting side pads and a securely fastened safety belt. The subject gripped an adjustable handle and moved the lever arm of the ergometer with a maximal voluntary contraction. For all dynamic contractions in the present investigation, the lever arm of the ergometer and hence, the forearm of the subject was set at an experimental starting position of 60 degrees with respect to the horizontal. The entire range of movement was 50 degrees.

A potentiometer was attached directly to the pivot axis of the lever arm of the ergometer and coincided with the axis of rotation of the subjects' elbow joint. The potentiometer was connected to a Honeywell Model 1706 Visicorder Oscillograph. Therefore, throughout the movement, the instantaneous angular displacement of the forearm as a function of time, was recorded.

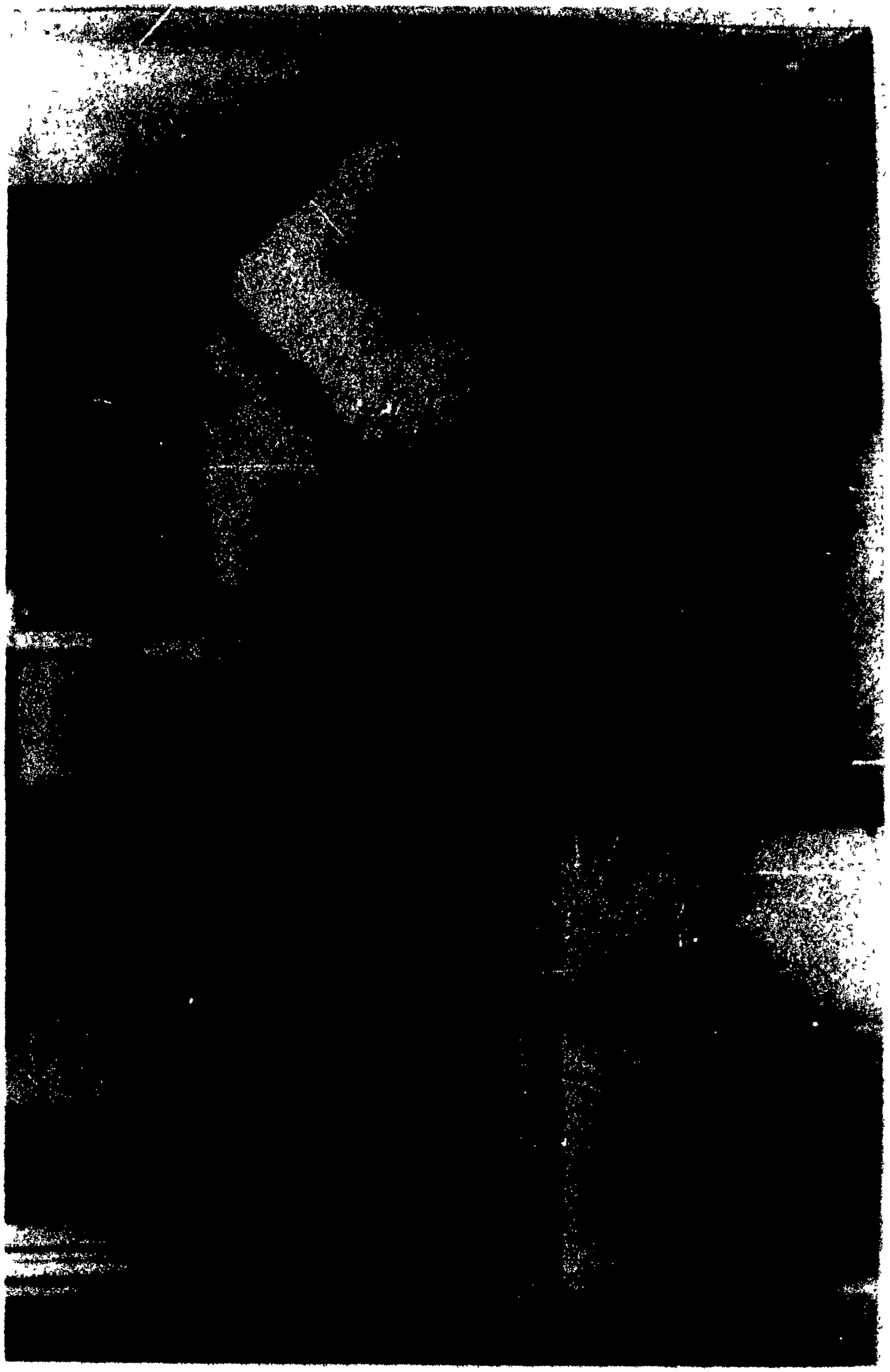
Force was exerted against a weight situated at a variable distance from the pivot axis of the resistance arm of the ergometer which was at a right angle to the lever arm. The lever and resistance arm of the ergometer was statically balanced with counterweights so that the subject worked against only the moment about the pivot axis generated by the weight plus the inertial forces of the frame structure and human forearm.

With the same weight, a series of different loads was obtained by moving the weight down the shaft of the resistance arm by a hand crank, away from the pivot axis of rotation. The distance the weight moved was accurately determined by a numerical counter, which corresponded to the number of revolutions taken by the crank. Therefore, the exact load could be reproduced between twin pairs. The ergometer is shown in Figure 1.

Maximal Linear Velocity under Loaded Conditions

On the basis of an initial record of the angular displacement of the forearm as a function of time, the

Figure 1:- The Ergometer and the Visicorder Oscillograph



maximal linear velocity (meters per second) was determined in the following manner. The slope of the tangent line of the angular displacement/time curve was calculated at an angle of 85 degrees with respect to the horizontal. This one angle was used because in all records analyzed, the slope of the tangent line became the steepest and was a straight line in the angular range of 80 to 90 degrees. Hence, angular velocity was maximal and constant within this range. The steepness of the slope of the tangent line was obtained by placing a front surface reflecting mirror across the curve at 85 degrees and turned until the reflection of the curve formed a straight line with the graph. A line was drawn along the edge of the mirror with a sharp pencil and the angle of this line was measured with a protractor. This angle was subtracted from 90 and the tangent of the subsequent angle calculated (17). The maximal angular velocity was therefore represented by equation (X):

$$\dot{\phi} = 100 \tan (90 - \phi) \qquad (X)$$

where: $\dot{\phi}$ = the maximal angular velocity (degrees per second);

100 = the paper speed of the visicorder (mm. per second); and

$(90 - \phi)$ = the slope of the tangent line (degrees).

The maximal angular velocity (degrees per second) was converted to radian measure by multiplying by 0.175. This value was multiplied by the radius of rotation of the subjects' forearm (elbow joint to the center of the palm in centimeters) and converted to its meter equivalent to obtain the maximal linear velocity in meters per second.

Maximal Palm Force under Loaded Conditions

The maximal palm force (Kg.) was always calculated for an angular displacement of the forearm at an angle of 85 degrees with respect to the horizontal, that is, at the same angle at which the maximal angular velocity was obtained (9,85). Since all angular velocities were maximal and constant over the range of 80 to 90 degrees, acceleration was zero and the maximal dynamic palm force was represented by equation (XI), the derivation of which is presented in Appendix B.

$$F_p = \frac{G_4 \times b \times \text{Sine } \phi}{C} \qquad \text{(XI)}$$

where:

F_p = the maximal palm force (Kg.), acting perpendicular to the resistance arm of the ergometer;

G_4 = the weight (Kg.) selected for the ergometer that supplied the load on the forearm;

b = the distance between the pivot axis of the ergometer and the center of gravity of the weight on the resistance arm. By geometry and construction of the ergometer, $b = 69.4 - 0.0232 \times r$, where r = the reading on a numerical counter which determined b distance;

ϕ = the angular displacement of the human forearm with respect to the horizontal (85 degrees); and

C = the distance (cm.) between the pivot axis of the elbow joint and the center of the palm of the hand.

One weight (G_4) was previously selected for the twin pair and was either 3.2, 6.5, or 9 kilograms throughout the series of different loads. All twin pairs received identical loads on the forearm flexor muscles. Previously selecting a weight was made necessary because if the weight used was too heavy for a given set of twins, only a small number of different loads could be obtained.

Maximal Linear Velocity (V_{max}) under Unloaded Conditions

An electrogoniometer (43) was attached with adhesive tape to the lateral side of the forearm and connected to the Honeywell Visicorder Oscillograph. In the experimental starting position of 60 degrees, the subject made a maximal voluntary flexion of the forearm throughout the entire range of 50 degrees without any load. The angular displacement of the forearm as a function of time was recorded and the maximal linear velocity under unloaded conditions (V_{max}) was determined by the same method as previously described for loaded conditions. Two measurements of V_{max} were made and the highest obtained maximal linear velocity (m. per second) was used as the experimental point of V_{max} on the force-velocity curve.

Maximal Isometric Force (P_o)

The lever arm of the ergometer was rigidly fixed at an angle of 80 degrees with respect to the horizontal. Isometric force has been shown (13) to be greatest at this angle and previous investigators (9,85) have used this angle when P_0 values have been determined for force-velocity curves of human forearm flexor muscles. A force dynamometer (Kg.) was inserted in the lever arm of the ergometer and adjusted to the forearm length of the subject. Two maximal voluntary contractions of the forearm flexor muscles were obtained with a three-minute rest period between the trials. The highest value attained was used as the experimental P_0 point on the force-velocity curve.

Maximal Muscular Power

The maximal force and velocity values, obtained at an angle of 85 degrees for a series of different loads, plus the maximal velocity of movement under unloaded conditions (V_{max}) and the maximal isometric force (P_0), provided the experimental points on which the force-velocity curve was drawn. For each twin, the force-velocity curve was drawn as the curve that "best fit" the experimentally obtained values. In only 4 twins, out of a total number of 34 force-velocity curves drawn, was the obtained maximal isometric force (P_0) less than what was predicted from the shape of the curve. In these cases, the force-velocity curve was extrapolated to a point that predicted the P_0 value from the shape of the curve.

Once the force-velocity curves were drawn, the maximal muscular power was calculated for each twin by obtaining the product of two variables; the maximal force (Kg.) and its corresponding maximal linear velocity (m. per second) for successive time intervals along the force-velocity curve. The product was multiplied by 60 and the maximal muscular power (Kg.m. per minute) was plotted and drawn on the same graph as the force-velocity curve.

Experimental Procedure

In a typical testing session, the twin brothers were given a medical examination which included a resting ECG. The form used by the examining doctor is presented in Appendix A.

The dominant arm of each twin was assessed by a series of questions which related to the more predominantly used arm for catching, writing, and in athletic events. The subject was seated in the ergometer and adjustments made so that the dominant arm was tested. The forearm was placed in a supine position and at the starting position of 60 degrees. The elbow joint was placed directly in line with the pivot axis of the arm of the ergometer and secured with adjustable side pads at the chest. The upper arm was maintained in line with the shoulders by an adjustable seat and arm rest. Finally, the upper body was prevented from moving by a safety belt.

An appropriate weight was selected for the ergometer and was moved up the shaft so that it was situated at the smallest distance from the pivot axis. The subject made four practise trials with the highest load at different speeds in order to familiarize himself with the movement of the lever arm.

The subject was instructed that he was to make a single maximal voluntary flexion of the forearm, rest three minutes, and then attempt another at a slightly heavier load. This procedure was to continue until he was unable to move the load over the entire range of 50 degrees. It was emphasized to the subject, that for each trial, a maximal effort must be given.

When the subject was ready to begin, the visicorder was immediately turned on by a hand extension and the subject made a maximal contraction of the forearm flexor muscles. During the three minute rest interval, the weight was moved down the shaft of the resistance arm of the ergometer and another maximal effort was recorded. In a few cases, the initial weight that was selected for the twin pair was too heavy and consequently, only a limited number of loads were obtained.

When the trials under loaded conditions terminated, an electrogoniometer was taped to the lateral side of the forearm and was placed in the starting position of 60 degrees. When the subject was ready, the visicorder was turned on and the maximal velocity of movement (V_{max}) under unloaded conditions was recorded. Another trial was taken after a three minute rest period.

The frame structure of the ergometer was then bolted in such a way that the lever arm remained fixed at an angle of 80 degrees. A force dynamometer was inserted in the lever arm and adjusted to the length of the subjects' forearm. When ready, the subject made a maximal voluntary contraction against the immovable force dynamometer. After three minutes rest, another maximal effort was obtained.

This procedure was followed for each twin pair. When both twins were finished the testing session, they were placed side by side and evaluated in terms of the physical similarity method of classification. The twins were then interviewed and a written record was kept as to their participation in athletics, leisure time activities, and family backgrounds. This completed the session which took approximately 4 to 6 hours per pair of twins.

After the results were analyzed, a special trip was made to the home of the twins in order to obtain the blood that was necessary for the determination of zygosity.

Calibration of the Apparatus

Ergometer

The ergometer was calibrated before each testing session. A pointer was fixed on the frame structure of the ergometer which pointed to a protractor that was fixed at the pivot axis but was allowed to rotate with the lever arm. The ergometer was calibrated such that an angular displacement of one degree for the lever arm, corresponded to a deflection of one millimeter on the visicorder.

Electrogoniometer

A protractor was attached to the electrogoniometer so that one shaft was immobilized while the other was free to move causing a change in angle. The electrogoniometer was calibrated before each testing session so that a one degree of change produced a deflection of one millimeter on the visicorder.

Force Dynamometer

The force dynamometer was calibrated by comparing the indicated output (Kg.) with known weights (Kg.) and linearity of the dynamometer was confirmed.

Statistical Treatment

Within-pair variance estimates for maximal muscular power, maximal velocity of movement, and maximal isometric force were generated separately for MZ and DZ twins by a one-way analysis of variance on the McGill Rax Terminal. If the within-pair variance F ratio ($\frac{W^2DZ}{W^2MZ}$) was significant at the 5% level of confidence, a heritability estimate (H_{est}) was derived for that variable from equation I.

$$H_{est} = \frac{W^2DZ - W^2MZ}{W^2DZ}$$

Coefficients of correlation were also obtained for the same three variables for MZ and DZ twins using the observed values between co-twin pairs.

Experimental Error

In Holzinger's formula (Equation I), the measurement error is reflected in the within-pair variance estimates for MZ and DZ twins.

CHAPTER IV

RESULTS

The partners of a twin pair were allocated by the first initial of the first and last name. The twin that demonstrated greater maximal muscular power was designated as partner A, while his twin brother was assigned as partner B.

Anthropometric data and zygosity determination of the male twins are presented in Table I.

Individual force-velocity curves for co-twin pairs along with the corresponding muscular power curves are shown in Figures 2 through 10 for MZ twins and Figures 11 through 18 for DZ twins.

The obtained values and intra pair differences for muscular power (MMP), maximal isometric force (P_o), and maximal velocity of movement (V_{max}) are presented in Table II for monozygotic twins, and Table III for dizygotic twins.

In Figures 19, 20 and 21, the observed values of MMP, P_o, and V_{max}, respectively, are plotted on a y-x system of co-ordinates for co-twin pairs. Correlation coefficients for the same variables are also given.

Within-pair variance estimates for MMP, P_o, and V_{max}, as generated by a one-way analysis of variance, are depicted in Table IV for the twins. The F ratios ($\frac{W^2DZ}{W^2MZ}$) for these variables are presented in Table V.

Heritability estimates (H_{est}) as derived from equation I are shown in Table V for maximal muscular power (H_{est} = 97%) and maximal isometric force (H_{est} = 83%).

TABLE I

ANTHROPOMETRIC DATA OF MZ AND DZ TWINS

Zygosity	Code		Age (yr)	Ht.(cm)	Wt.(kg)
MONOZYGOTIC	BG	A	11	152	36
	BG′	B	11	152	36
	DA	A	14	167.2	45
	RA	B	14	165	52.7
	DM	A	15	151.5	45
	RM	B	15	155	52.7
	MT	A	14	156.4	48.1
	PT	B	14	159.2	46
	DO	A	11	140	37.5
	RO	B	11	141	39
	BD	A	15	168.2	54
	GD	B	15	166	56.7
	JB	A	12	143.5	39.2
	JB′	B	12	145.5	40.7
	PR	A	15	167	70
	PR′	B	15	167	67.7
	MG	A	14	162.5	52.2
	JG	B	14	154	46.3
	MEAN		13.4	156.3	48.0
	± SD		1.6	9.6	9.9
	RANGE		4	28.2	34
DIZYGOTIC	KW	A	11	142.3	39
	TW	B	11	136	36
	GP	A	11	141.5	38
	GP′	B	11	146	42
	DL	A	17	168	72
	CL	B	17	160	65
	NB	A	11	141.5	46.1
	MB	B	11	147	56.7
	FG	A	12	153.5	45.5
	JG	B	12	143.2	35.4
	BC	A	13	159	56.3
	SC	B	13	150	50
	TS	A	12	152	46.3
	DS	B	12	140	39.2
	PN	A	13	166	58.7
	BN	B	13	159	44
	MEAN		12.5	150.3	48.1
	± SD		1.9	9.8	10.8
	RANGE		6	32	22.7

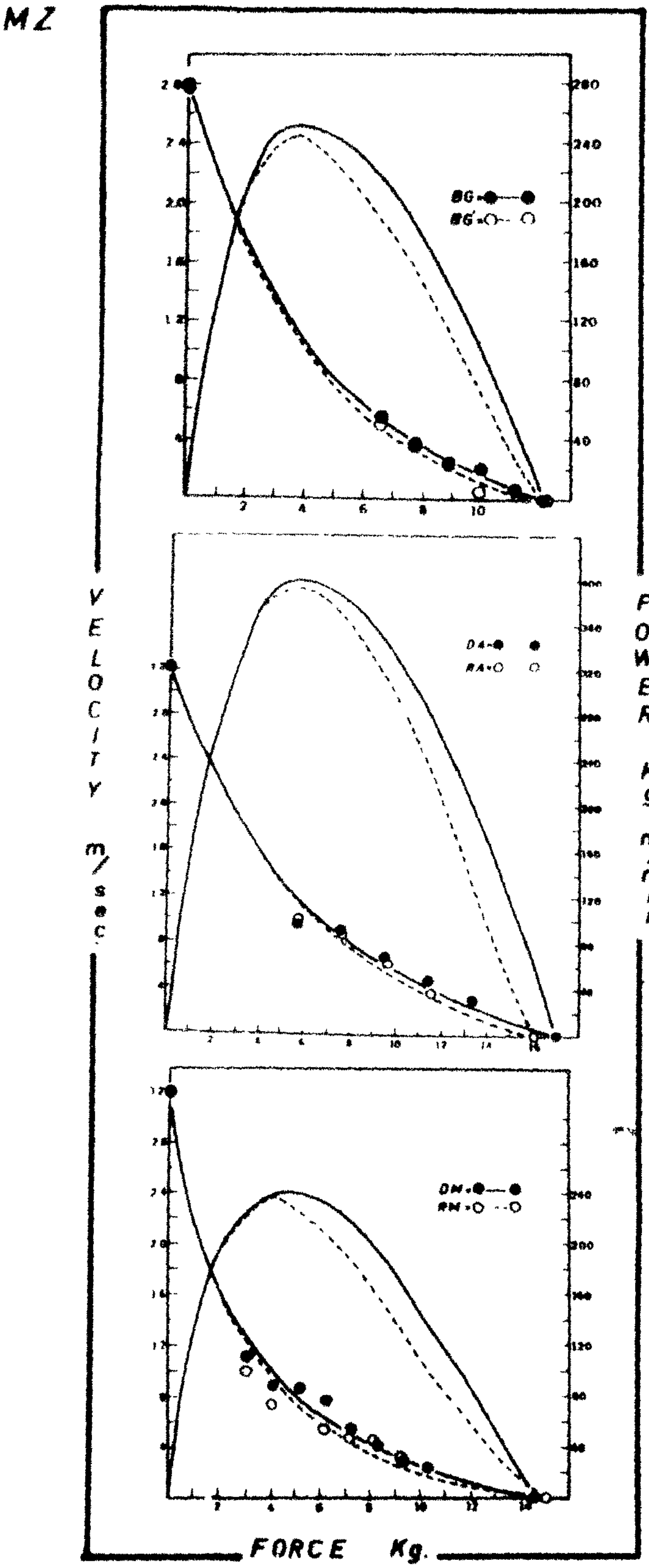


Figure 2.

Figure 3.

Figure 4.

Force-Velocity and Maximal Muscular Power Curves
for Monozygotic Twins

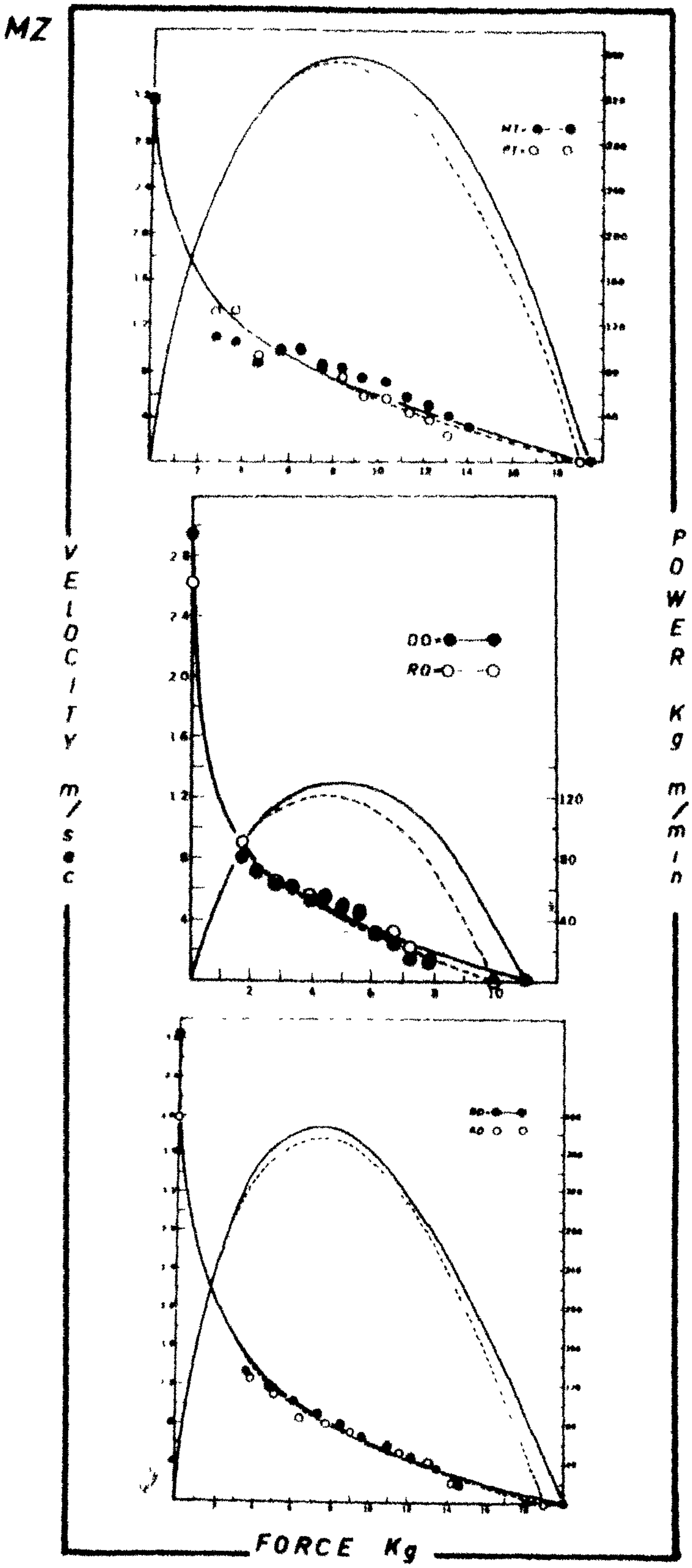


Figure 5.

Figure 6.

Figure 7.

Force-Velocity and Maximal Muscular Power Curves
for Monozygotic Twins

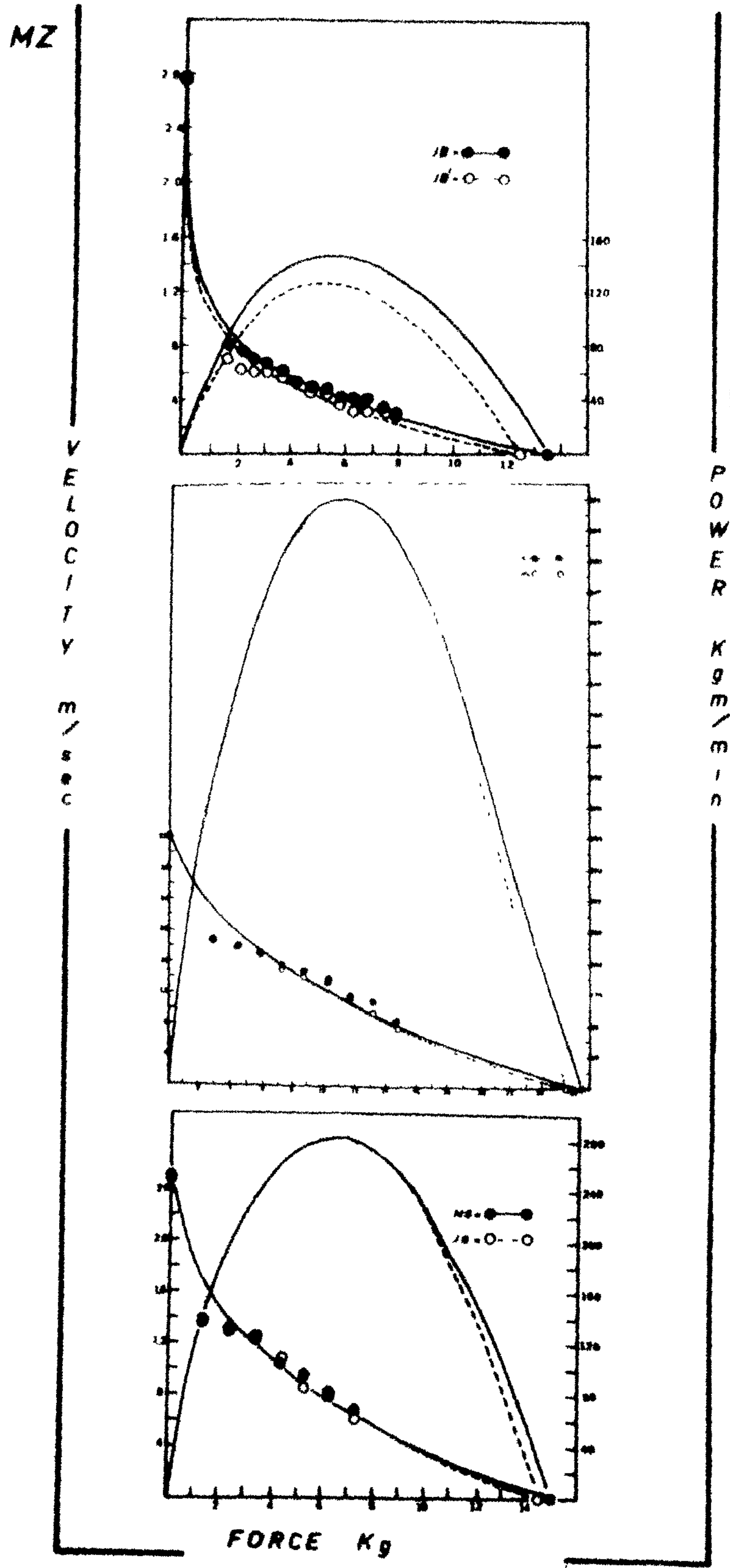


Figure 8.

Figure 9.

Figure 10.

Force-Velocity and Maximal Muscular Power Curves
for Monozygotic Twins

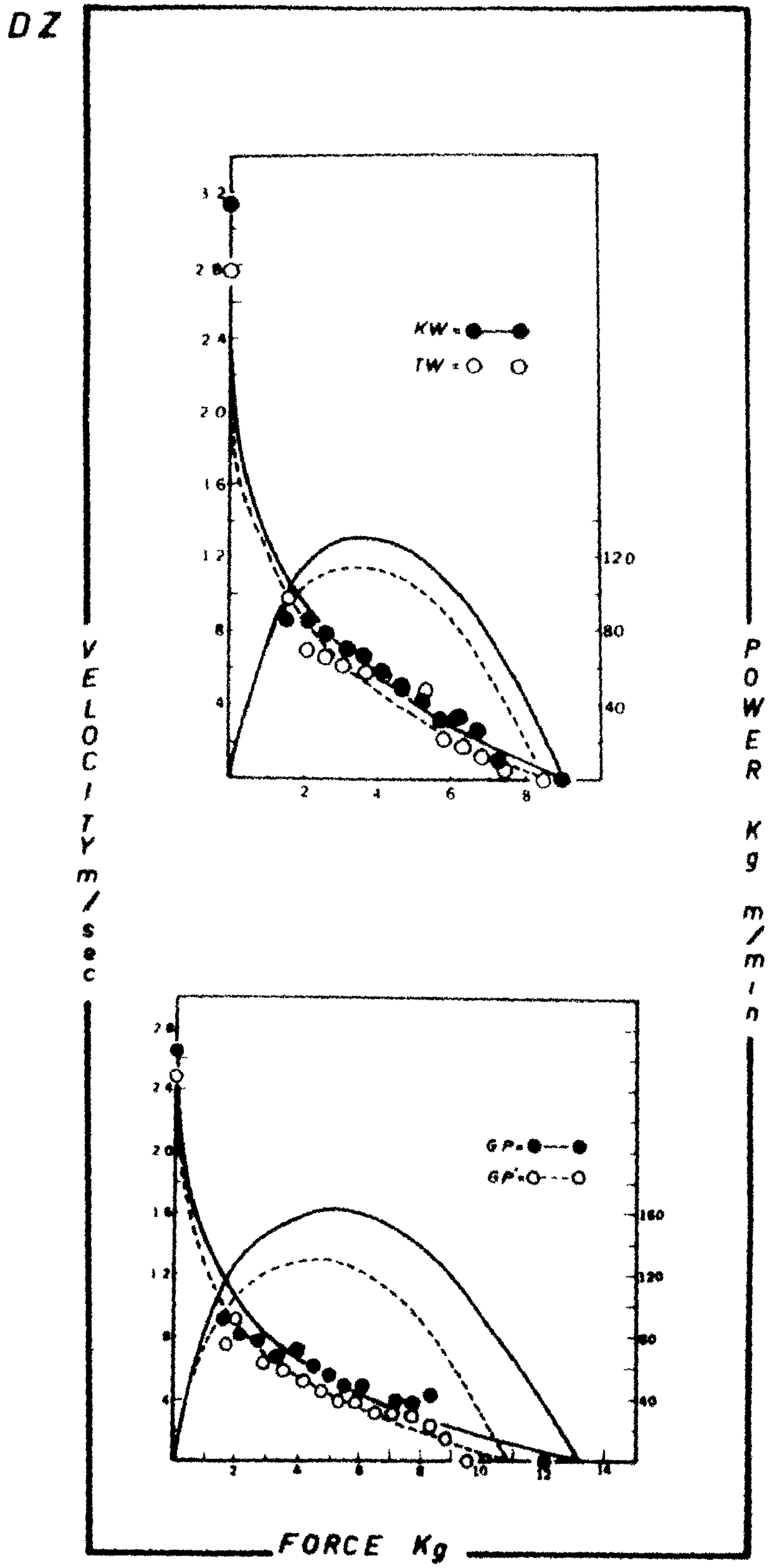


Figure 11.

Figure 12.

Force-Velocity and Maximal Muscular Power Curves
for Dizygotic Twins

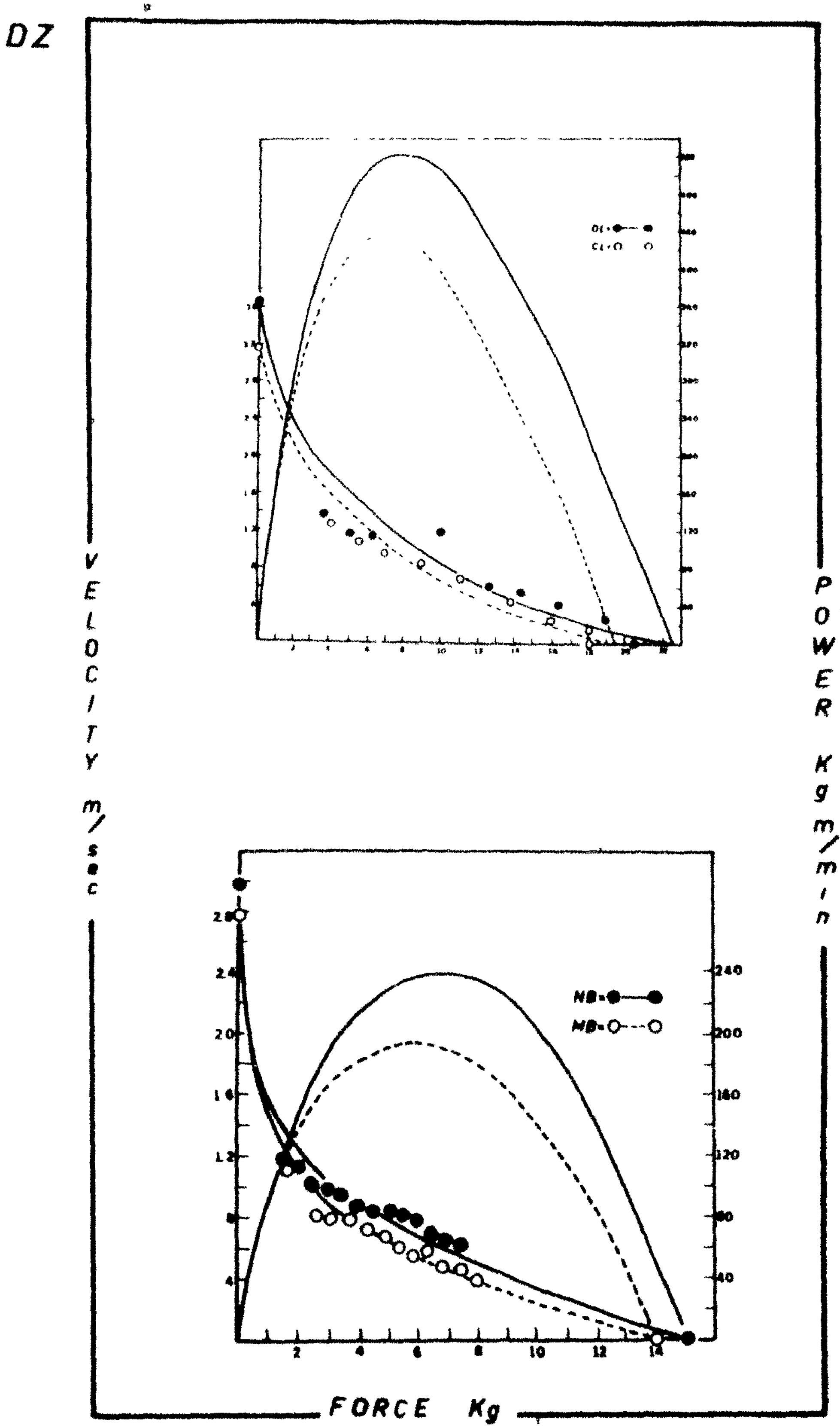


Figure 13.

Figure 14.

Force-Velocity and Maximal Muscular Power Curves
for Dizygotic Twins

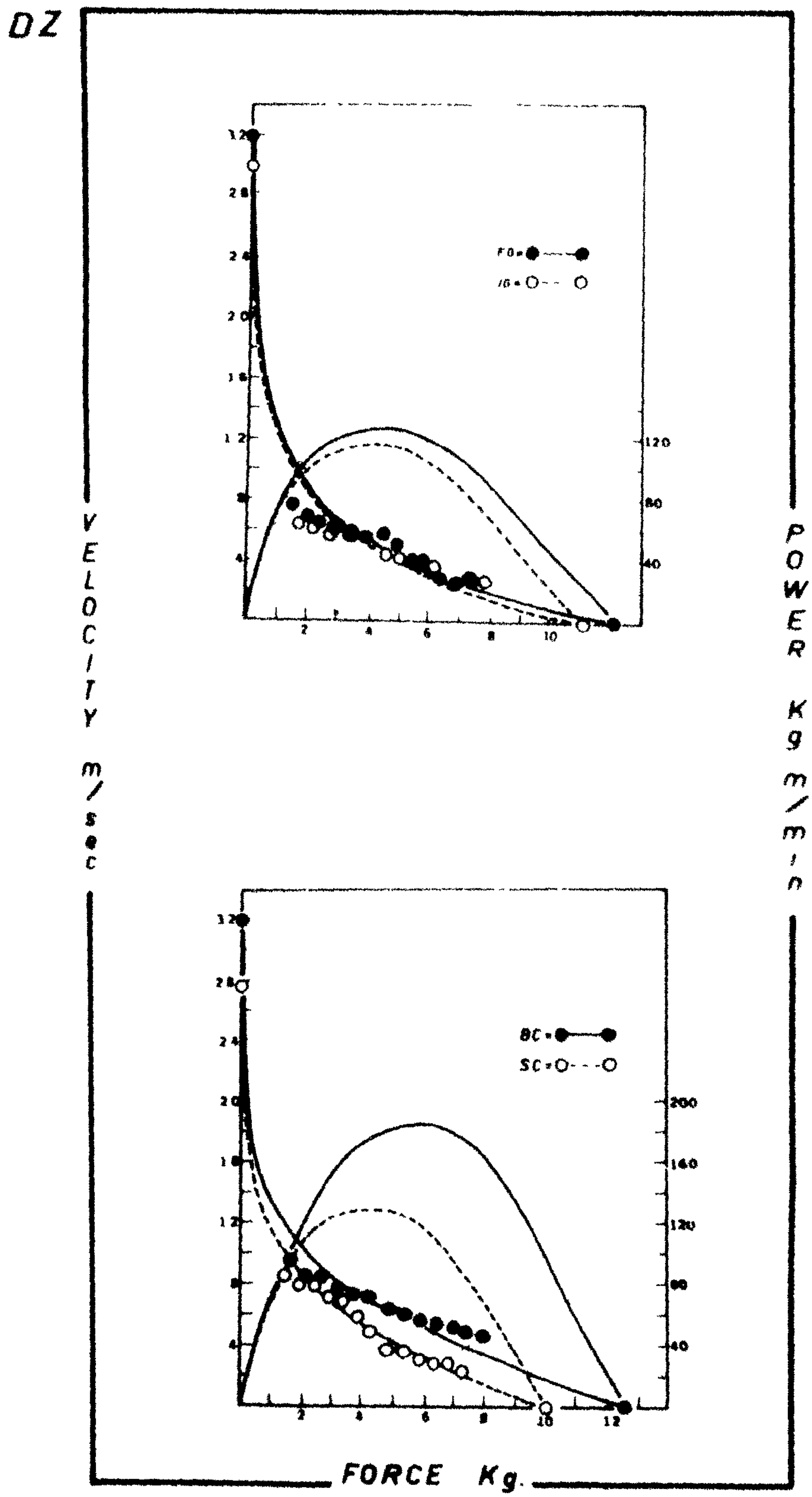


Figure 15.

Figure 16.

Force-Velocity and Maximal Muscular Power Curves for Dizygotic Twins

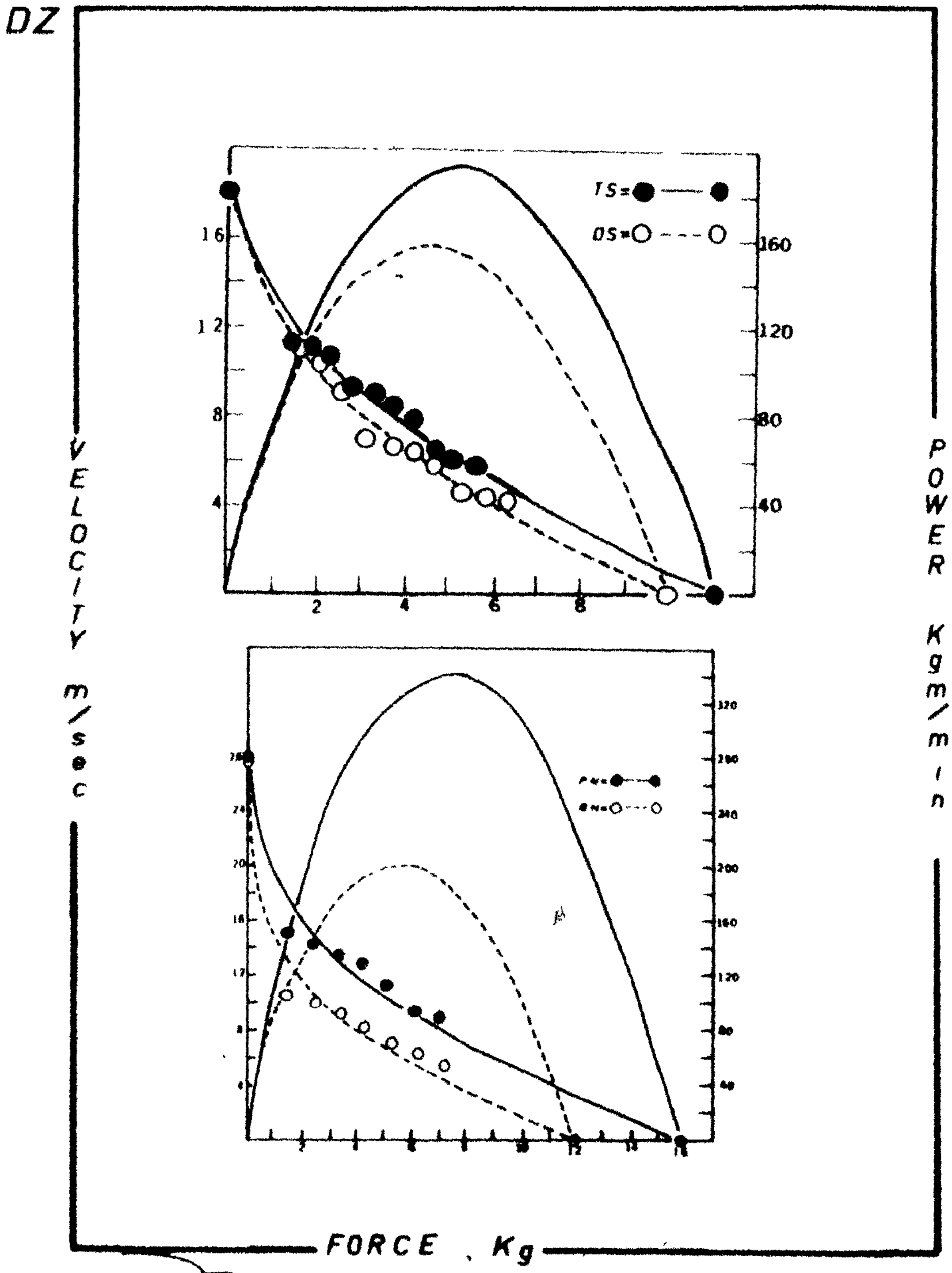


Figure 17.

Figure 18.

Force-Velocity and Maximal Muscular Power Curves
for Dizygotic Twins

TABLE II

MAXIMAL VELOCITY OF MOVEMENT, MAXIMAL ISOMETRIC FORCE AND MAXIMAL MUSCULAR POWER OF MONOZYGOTIC TWINS

Zygosity	Code		V_{max}(m/sec)	Diff	P_o(kg)	Diff	MMP(kgm/m)	Diff
MONOZYGOTIC	BG	A	2.78	0	12	0	252	
	BG'	B	2.78		12		244.8	7.2
	DA	A	3.21	0	17	1	399.6	7.2
	RA	B	3.21		16		392.4	
	DM	A	3.20	0	15	.5	240	4.4
	RM	B	3.20		14.5		235.6	
	MT	A	3.17	0	19.5	.5	355	9.4
	PT	B	3.17		19		345.6	
	DO	A	2.92	.29	11	1	129	7.4
	RO	B	2.63		10		121.6	
	BD	A	4.84	.56	20	1	386.4	12.4
	GD	B	3.98		19		374	
	JB	A	2.77	0	13.5	1	144	21
	JB'	B	2.77		12.5		123	
	PR	A	3.22	0	26.5	1	759	7
	PR'	B	3.22		25.5		752	
	MG	A	2.51	0	15	1	280.8	0
	JG	B	2.51		14		280.8	
Mean			3.12		16.2		323.1	
± SD			.56		4.6		183.5	
Range			2.33		16.5		637.4	

TABLE III

MAXIMAL VELOCITY OF MOVEMENT, MAXIMAL ISOMETRIC FORCE AND MAXIMAL MUSCULAR POWER OF DIZYGOTIC TWINS

Zygosity	Code		V_{max}(m/sec)	Diff	P_o(kg)	Diff	MMP(kgm/m)	Diff
DIZYGOTIC	KW	A	3.14	.37	9	.5	130	15
	TW	B	2.77		8.5		115	
	GP	A	2.65	.17	12	2.5	162	32.4
	GP'	B	2.48		9.5		129.6	
	DL	A	3.65	.52	20.5	2.5	523.2	87.2
	CL	B	3.13		18		436	
	NB	A	2.97	.20	15	1	239.4	45.4
	MB	B	2.77		14		194	
	FG	A	3.20	.20	12	1	126	10.8
	JG	B	3.00		11		115.2	
	BC	A	3.20	.43	12	2	187.2	60
	SC	B	2.77		10		127.2	
	TS	A	1.82	.02	11	1	195	39
	DS	B	1.80		10		156	
	PN	A	2.83	.07	16	4	340.8	139.2
	BN	B	2.76		12		201.6	
Mean			2.81		12.51		211.1	
± SD			.48		3.37		120.6	
Range			1.85		12.0		408.2	

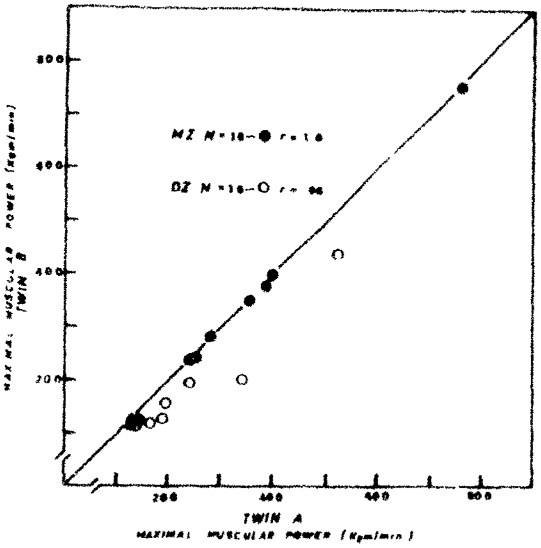


Figure 19.

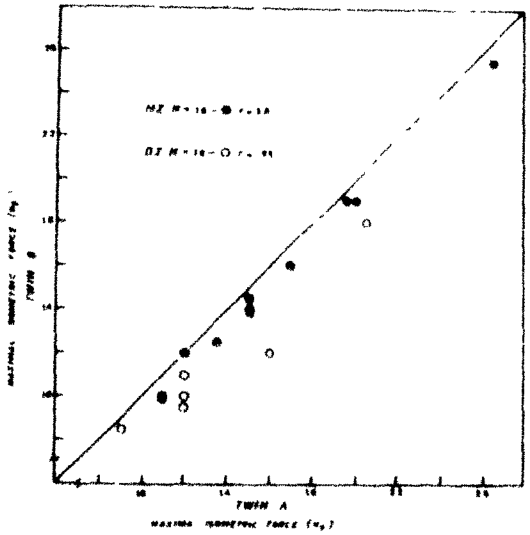


Figure 20.

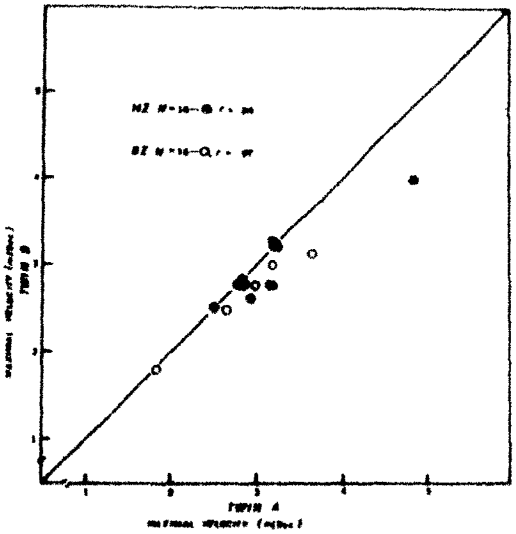


Figure 21.

Intrapair Values for Maximal Muscular Power, Maximal Isometric Force (P_0) and Maximal Velocity (V_{max})

TABLE IV

ESTIMATES OF WITHIN VARIANCE FOR MZ AND DZ TWINS

Variable No. 1	Maximal Muscular Power (MMP)		
	Source of Variation	DF	VAR EST
Within (MZ)	455.00	8	50.56
Within (DZ)	17777.12	7	2222.14
Variable No. 2	Maximal Isometric Force (P_o)		
	Source of Variation	DF	VAR EST
Within (MZ)	3.25	8	0.36
Within (DZ)	17.88	7	2.23
Variable No. 3	Maximal Velocity (V_{max})		
	Source of Variation	DF	VAR EST
Within (MZ)	0.41	8	0.05
Within (DZ)	0.35	7	0.04

TABLE V

HERITABILITY ESTIMATES

	$F = \frac{W^2DZ}{W^2MZ}$	%Heritability Estimate
Maximal Muscular Power (kgm/min)	43.95*	97%
Maximal Isometric Force (Kg)	6.19*	83%
Maximal Velocity (m/sec)	.80+	

* Significant at 01 level

\+ Not significant at .05 level

CHAPTER V

DISCUSSION

Interpretation of twin data requires that both the validity and the true meaning of the heritability estimate (H_{est}) be considered. The H_{est} is based on the thesis of comparable pre and postnatal environmental influences between MZ and DZ twins and nil heredity-environment interaction. The tenability of accepting these assumptions has been previously discussed (Chapter I). Suffice to say here, that these assumptions may be open to serious question when psychological traits are the subject of investigation (77), but when physiological variables are measured as in the present study, then the acceptability of these assumptions can be substantiated (4,47,50,77). To strengthen the acceptance further, emphasis must be placed on the fact that extreme care was observed in obtaining comparable MZ and DZ groups with regard to their socio-economic backgrounds, leisure time activities, age, and physical endeavours. From the written records kept of the interview with the twins, only one MZ pair (PR and PR') (Figure 9), appeared to diverge in a physical activity which might have produced an exaggerated within-pair variance estimate for the three variables under study. One twin (PR), was involved in a heavy weight training program. However, Figure 9 reveals extremely high values for maximal muscular power, maximal isometric force, and maximal velocity of contraction, with very small intra-pair differences (Table II). Klissouras (46) has suggested that "rigorous athletic training cannot contribute to functional development beyond a limit set by the genotype" (46). Possible hereditary factors may have overided the influence of the weight training program for this set of twins.

With regard to the true value of H_{est}, broad generalizations and inferences about the relative powers of heredity and environment have to be avoided. It is erroneous to believe that a H_{est} value signifies to what extent a trait is genetically determined. The H_{est} is only an estimate of the extent to which interindividual variation in heredity affects the variation of a given organic attribute, in a given population exposed to similar environmental influences, at a given time (46).

The individual force-velocity curves (Figures 2 through 18) have followed the classical exponential form (9,35,49, 85). Further, the maximal muscular power curves, as derived from the individual force-velocity curves, have added support to the result of Ikai (35), that the maximum power of the forearm flexor muscles is found when the force and velocity values are approximately 35% of the maximum values.

The accuracy of the obtained results (Table II and III) for maximal muscular power (MMP) depend upon the precision with which the force-velocity curves were drawn to "best fit" these experimentally obtained values. Only 2 sets of twins (Figures 12 and 13) revealed a lower maximal isometric force (P_o) than that predicted by extrapolation of the force-velocity curve to zero velocity. Fatigue factors, brought about by the great number of different loads that were used, may have contributed to these lesser observed values for P_o. In addition, proceeding from the lightest towards the heaviest load, instead of in the reverse direction as some other investigations have done (30,85) may have added to the muscular fatigue and contributed to these lesser P_o values as well. In Figures 2 and 3, only 6 loads were obtained because the previously selected weight was too heavy and only a limited range of loads were available. In these two cases, the accuracy of the force-velocity-power curves may be questioned. However, all other force-velocity curves were based on a substantial number of different loads which made the drawing of the "best fit" curve more precise.

Close inspection of the force-velocity-power curves indicated that the intra-pair differences for MMP appear to be greater between DZ co-twin pairs than MZ co-twin pairs. Further, the greater intrapair differences of the DZ twins are a direct result of individual differences in the relative position of the force-velocity curve. The intra-pair differences (Table II and III) are further exemplified when the values for co-twin pairs are plotted on a y-x system of coordinates as depicted in Figures 19, 20 and 21. These figures reveal that MZ co-twin pairs obtained a perfect correlation (r=1.0) for maximal muscular power and maximal isometric force as opposed to .96 and .95 for the DZ co-twin pairs. However, DZ co-twin pairs obtained a higher correlation (r=.97) for maximal velocity of movement (V_{max}) than did MZ co-twin pairs (r=.94).

Maximal velocity of movement under unloaded conditions (V_{max}) has demonstrated interindividual variability (85) but the investigator stated that "the maximum velocity of movement was relatively constant". In this regard, Komi (50), did not observe a significant difference between MZ and DZ twins in the maximal running velocity on a staircase. Therefore, it was not surprising to find that the F ratio ($\frac{W^2DZ}{W^2MZ}$) for maximal velocity of movement of the forearm was not statistically significant. Consequently, the calculation of the heritability estimate was abandoned.

Interindividual variation in maximal isometric force has been clearly demonstrated (9,13,36,85). However, Komi (50) failed to find significant intrapair differences between MZ and DZ twins for this variable using the forearm flexor and quadriceps muscles. The present investigation, found that the F ratio ($\frac{W^2DZ}{W^2MZ}$) for maximal isometric force of the forearm flexor muscles was significant at the .01 level of confidence. From the heritability estimate derived (Table V) it appears that the variation in maximal isometric force is 83% determined by heredity. It is difficult to conceive of a reasonable explanation that will offer a solution to this disagreement. Ikai and Fukunage (36) have demonstrated by means of ultrasonic measurement, that the strength of a muscle is proportional to the cross sectional area of the muscle. In this respect, it seems reasonable to assume that DZ co-twin pairs would have a greater intra pair difference in the size of the flexor muscles and therefore would have a greater within-pair variance estimate for maximal isometric force.

Interindividual variability in maximal muscular power has been shown to be governed by individual differences in the relative position of the force-velocity curve (35). The heritability estimate derived for maximal muscular power will therefore reflect the extent to which variation in the position of the force-velocity curve is determined by variation in heredity. The F ratio $(\frac{W^2DZ}{W^2MZ})$ for maximal muscular power was significant well beyond the .01 level of confidence. The high heritability estimate (97%) for maximal muscular power (Table V), indicates the extreme extent to which the observed variation in this organic attribute is subject to variation in heredity. The result concurs with the investigation of Komi, Klissouras, and Karvinen (50), who reported a H_{est} value of 99.2%. The experimentors suggested "that the variance in maximal muscular power may not be due to an individual difference in the splitting rate of high energy phosphate compounds, but to a quantum, that is, to a greater amount of adenosine triphosphate and phosphocreatine which are made available as a result of a greater mass of protoplasmic tissue". This explanation appears plausible for maximal muscular power obtained from a maximal effort which required continuous contractions as does running on a staircase. It is difficult to conceive that depletion of phosphocreatine applied to the present investigation. Maximal muscular power curves were obtained from single maximal contractions of approximately one second with a three minute rest period between each contraction. Rephosphorylation of ADP and thus of phosphocreatine from both glycolytic and respiratory activity of the forearm flexor muscles would clearly have been completed within the rest interval. Huxley (34) has stated that "the most likely seat of the force-developing mechanism is the globular part of the heavy meromyosin and its attachment to the actin filaments". The interindividual variation observed in maximal muscular power in the present study may be the result of individual differences in the total number of these reactive sites that are allowed to take part during a maximal effort under loaded conditions. To strengthen this supposition, Ikai and Fukunage (36) have shown that by training the forearm flexor muscles, the increase in maximum strength is associated with an increase in the cross sectional area and the strength per unit cross sectional area of the muscle While this does not suggest a direct increase in the amount of contractile element, it does suggest that a greater number of reactive sites took part in the maximal effort.

The high heritability estimate (97%) for maximal muscular power of the forearm flexor muscles indicates that the interindividual variation in the relative position of the force-velocity curve is also governed by the same variation in heredity (97%). With this in mind, physical educators, coaches and trainers must begin to think in terms of the training of the force-velocity curve rather than the training of muscle power. Ikai (35) has demonstrated that the greatest displacement of the force-velocity curve takes place with a subsequently greater increase in maximal muscular power if the load used in dynamic training is 30 to 60% of the maximum isometric force. In this manner, the individuals may work toward "the ideal pattern of force-velocity relationship specific to each athletic event" (35).

CHAPTER VI

SUMMARY AND CONCLUSIONS

Summary

The purpose of this investigation was to ascertain to what extent variation in heredity contributes to interindividual variation in the force-velocity relationship of human muscle. More specifically, the twin study method of research was employed for the purpose of attempting to derive heritability estimates for: the maximal muscular power developed by the forearm flexor muscles as derived from individual force-velocity curves; the maximal velocity of movement (V_{max}) of the forearm produced by the contracting forearm flexor muscles under unloaded conditions and; the maximal isometric force (P_0) produced by the forearm flexor muscles at an elbow angle of 80°.

Male monozygotic twins (N=9 pairs) and like sexed dizygotic twins (N=8 pairs) participated in the study. Their ages ranged from 11 to 17 years. Zygosity determination was made by the physical similarity method of classification and a blood and serum examination. The co-twin pairs were obtained from greater metropolitan Montreal, lived at home with their parents, and had similar leisure time activities.

A specially designed ergometer allowed the determination of the force-velocity relationship of the forearm flexor muscles as they collectively exerted their force at the palm of the hand. From an experimental starting position of 60° with respect to the horizontal, each co twin pair made a single voluntary maximal flexion of the forearm flexor muscles for a series of different loads. The entire range of movement was 50 degrees. All co twin pairs received identical loads with a three minute rest interval between the different loads. The maximal exerted palm force (Kg.) and its corresponding maximal linear velocity (m/sec) were obtained from an initial angular displacement/time curve. It was found that within the angular range of 80-90 degrees that all the slopes of the angular displacement/time curves were the steepest and a straight line. Hence, all force and velocity values were calculated for an angular displacement of 85 degrees with respect to the horizontal. The maximal exerted palm force and its corresponding maximal linear velocity for the series of different loads provided the experimental points for the force velocity curves.

Maximal linear velocity of movement (V_{max}) under unloaded conditions was obtained with an electrogoniometer strapped to the lateral side of the forearm which recorded an angular displacement/time curve throughout the same range as for the loaded conditions. All measurements of V_{max} were made at an angular displacement of 85 degrees.

Maximal isometric force was obtained from a force dynamometer inserted in the ergometer which was fixed at an angle of 80 degrees. Maximal isometric force and V_{max} provided additional points of reference on which the "best fit" force-velocity curves were drawn.

The maximal muscular power (Kgm/min) curves were calculated from the "best fit" force-velocity curves.

Within-pair variance estimates were generated separately for MZ and DZ twins by a one way analysis of variance for maximal muscular power (MMP), maximal isometric force (P_o), and maximal velocity of movement (V_{max}). If the within-pair variance ratio ($F = \frac{W^2DZ}{W^2MZ}$) was statistically significant, heritability estimates (H_{est}) were derived from Equation I.

$$H_{est} = \frac{W^2DZ - W^2MZ}{W^2DZ}$$

The heritability estimate calculation was abandoned for maximal velocity (V_{max}) because the F ratio ($\frac{W^2DZ}{W^2MZ}$) was not statistically significantly different between MZ and DZ twins. However, it was found that the within-pair variance ratio for maximal muscular power (Kgm/min) and maximal isometric force (Kg) was significantly different between MZ and DZ twins at the .01 level of confidence ($F = 43.95$ and 6.1, respectively). Consequently, heritability estimates for these variables were derived from Equation 1 and yielded a value of 97% for maximal muscular power and 83% for maximal isometric force.

Conclusions

On the basis of the statistical analysis, the following conclusions are justifiable:

(1) Interindividual variability in maximal isometric

force of the forearm flexor muscles at an angle of 80 degrees is 83% determined by variation in heredity in a homogeneous population exposed to similar environmental influences;

(2) Interindividual variability in maximal muscular power of the forearm flexor muscles is 97% determined by variation in heredity in a homogeneous population exposed to similar environmental influences;

(3) Interindividual differences in maximal muscular power of the forearm flexor muscles are governed by the observed differences in the relative position of the force-velocity curve. Therefore, it is concluded that the interindividual variability observed in the force-velocity relationship of the forearm flexor muscles is governed almost entirely by variation in heredity in a homogeneous population exposed to similar environmental influences.

BIBLIOGRAPHY

1. Abbot, B. C., and J. Lowy. Contraction in Molluscan Smooth Muscle. J. Physiol., 141: p. 385, 1958.

2. Abbot, B. C., and D. R. Wilkie. The Relation Between Velocity of Shortening and the Tension - Length Curve of Skeletal Muscle. J. Physiol., 120: p. 214, 1953.

3. Anastasi, A., and J. P. Foley Jr. A Proposed Reorientation in the Hereditary - Environment Controversy. Psychol. Review, 55: p. 239, 1948.

4. Arkinstall, W. W., K. Nirmel, V. Klissouras, and J. Milic - Emili. Genetic Differences in the Ventilatory Response to Inhaled CO_2. J. Appl. Physiol., 36: p. 6, 1974.

5. Bender, S., Twins and Heredity. The Practitioner, 283: p. 183, 1959.

6. Best, C. H., and R. C. Partridge. The Equation of Motion of a Runner Exerting a Maximal Effort. Roy. Soc. Proc., B, 103: p. 218, 1928.

7. Clark, P. J., The Heritability of Certain Anthropometric Characteristics as Ascertained from Measurement of Twins. Amer. J. Human Genetics, 8: p. 49, 1956.

8. Davidson, E. H., Hormones and Genes. Scientific Amer., 212: p. 36, 1965.

9. Dern, R. J., J. M. Levene, and H. A. Blair. Forces Exerted at Different Velocities in Human Arm Movements. Amer. J. Physiol., 151: p. 415, 1947.

10. Diaz, M., and C. Pavan. Changes in Chromosomes Induced by Micro-organism Infection. Proc. National Acad. Sci., 54: p. 1321, 1965.

11. Dickenson, S., The Dynamics of Bicycle Pedalling. Proc. Roy. Soc., B, 103: p. 225, 1928.

12. Doi, Y., Studies on Muscular Contraction: the Relation Between the Maximal Work and the Tension Developed in a Muscle Twitch, and the Effects of Temperature and Extension. J. Physiol., 54: p. 335, 1921.

13. Doss, W. S., and P. V. Karpovich. A Comparison of Concentric, Eccentric, and Isometric Strength of Elbow Flexors. J. Appl. Physiol., 20: p. 351, 1965.

14. Dubois, R., Nature and Nurture. In Progress in Medical Genetics. Chap. 1. Ed. by A. G. Steinberg, and A.G. Bearn. Grune and Stratton, New York and London, 5: 1967.

15. Eysenck, H. J., and D. B. Prell. The Inheritance of Neuroticism, an Experimental Study. J. Mental Sci., 97: p. 411, 1951.

16. Fenn, W. O., Functional and Kinetic Factors in the Work of Sprint Running. Amer. J. Physiol., 92: p. 583, 1930.

17. Fenn, W. O., and B. S. Marsh. Muscular Force at Different Speeds of Shortening. J. Physiol., 85: p. 277, 1935.

18. Fenn, W. O., H. Brody, and A. Petrilli. The Tension Developed by Human Muscles at Different Velocities of Shortening. Amer. J. Physiol., 97: p. 1, 1931.

19. Ferreira, A. J., Emotional Factors in Prenatal Environment. J. Nerv. Mental Dis., 141: p. 108, 1965.

20. Furusawa, K., A. V. Hill, and J. L. Parkinson. The Dynamics of Sprint Running. Roy. Soc. Proc., B, 102: p. 29, 1927.

21. Galton, F., The History of Twins as a Criterion of the Relative Powers of Nature and Nurture. Fraser's Magazine, 12: p. 566, 1875.

22. Gasser, H. S., and A. V. Hill. The Dynamics of Muscular Contraction. Roy. Soc. Proc., B, 96: p. 398, 1924.

23. Goldberg, M. L., and W. A. Atchley. The Effect of Hormones on DNA. Proc. National Acad. Sci., 55: p.989, 1966.

24. Gorini, L., Antibiotics and the Genetic Code. Scientific Amer., 214: p. 102, 1966.

25. Hansen, T. E., and J. Lindhard. On the Maximal Work of Human Muscles Especially the Flexors of the Elbow. J. Physiol., 57: p. 287, 1923.

26. Hartree, W., and A. V. Hill. The Factors Determining the Maximum Work and the Mechanical Efficiency of Muscle. Proc. Roy. Soc., B, 103: p. 234, 1928.

27. Hill, A. V., The Efficiency of Mechanical Power Development during Muscular Shortening and its Relation to Load. Proc. Roy. Soc., B, 159: p. 319, 1964.

28. Hill, A. V., The Heat of Shortening and the Dynamic Constants of Muscle. Proc. Roy. Soc., B, 126: p. 136, 1938.

29. Hill, A. V., An Instrument for Recording the Maximum Work in Muscular Contraction. J. Physiol., 53: 1920.

30. Hill, A. V., The Maximum Work and Mechanical Efficiency of Human Muscles and their Most Economical Speed. J. Physiol., 56: p. 19, 1922.

31. Hill, A. V., Trails and Trials in Physiology. Baltimore. The Williams and Wilkins Company, p. 137, 1965.

32. Hill, A. V., C. N. H. Long, and H. Lupton. The Effect of Fatigue on the Relation Between Work and Speed in the Contraction of Human Arm Muscles. J. Physiol., 58: p. 334, 1926.

33. Holzinger, K. J., The Relative Effect of Nature and Nurture Influences on Twin Differences. J. Educ. Psychol., 54: p. 231, 1929.

34. Huxley, H. E., The Mechanism of Muscular Contraction. Science, 164: p. 1356, 1969.

35. Ikai, M., Training of Muscle Strength and Power in Athletes. Paper Presented at the XVIIIth World Congress of Sports Medicine, Oxford, Sept., 1970.

36. Ikai, M., and T. Fukunaga. A Study on Training Effect on Strength Per Unit Cross-Sectional Area of Muscle by Means of Ultrasonic Measurement. Int. Z. Angew Physiol., 28: p. 173, 1970.

37. Jensen, A. R., How Much can we Boost I.Q. and Scholastic Achievement? *Howard Educational Review*, 39: No. 1, 1969.

38. Joffe, J. M., Genotype and Prenatal and Primating Stress Interact to ffect Adult Behavior in Rats. *Science*, 150: p. 1844, 1965.

39. Johnson, R. C., Similarity in I.Q. of Separated Identical Twins as Related to Length of Time in Same Environment. *Child Development*. 34: p. 745, 1963.

40. Jones, H. E., and P. T. Wilson. Reputation Differences in Like-Sex Twins. *J. Exper. Educ*. 1: p. 86, 1932.

41. Jost, J., and L. Sontag. The Genetic Factor in Autonomic Nervous System Function. *Psychosomatic Medicine*, 6: p. 308, 1944.

42. Juel-Nielsen, N., A. Nielsen, and M. Hange. On the Diagnosis of Zygosity in Twins and the Value of Blood Groups. *Acta. Genet*., 8: p. 256, 1950.

43. Karpovich, P. V., E. L. Herden, and M. M. Asa. Electrogoniometric Study of Joints. *United States Armed Forces Med. J*., 11: p. 424, 1960.

44. Katz, B., The Relation Between Force and Speed in Muscular Contraction. *J. Physiol*., 96: p. 45, 1939.

45. Kelley, D. L., *Fundamentals of Motion Description*. Prentice Hall Inc., Englewood Cliffs, New Jersey, 1971.

46. Klissouras, V., Heredity and Training: Twin Studies. A Paper Submitted to the Medical Journal DUODECIM for its Special Issue on Sports Medicine, April 24, 1973.

47. Klissouras, V., Heritability of Adaptive Variation. *J. Appl. Physiol*., 31: p. 3, 1971.

48. Klissouras, V., Prediction of Potential Performance with Special Reference to Heredity. *J. Sports Med*., 13: No. 2, p. 100, 1973.

49. Komi, P. V., Measurement of the Force-Velocity Relationship in Human Muscle under Concentric and Eccentric Contractions. A Paper Presented at the IIIrd International Seminar on Biomechanics, Rome, Sept., 1971.

50. Komi, P. V., V. Klissouras, and E. Karvinen. Genetic Variation in Neuromuscular Performance. Int. Z. angew Physiol., 31: p. 289, 1973.

51. Kryshova, N. A., Z. V. Beliaeva, A. F. Dmitrieva, M. A. Zhilinokaie, and L. G. Pernov. Investigation of the Higher Nervous Activity and of Certain Vegetative Features in Twins. Soviet Psychology and Psychiatry, 1: p.36, 1963.

52. Lennox, W. G., F. A. Gibbs, and F. L. Gibbs. The Brain Wave Pattern, an Hereditary Trait: Evidence from 74 "Normal" Pairs of Twins. J. Heredity, 36: p. 233, 1945.

53. Levin, A., and J. Wyman. The Viscous Elastic Properties of Muscle. Roy. Soc. Proc., B, 101: p. 218, 1927.

54. Lupton, H., The Relation Between the External Work and the Time Occupied in a Single Muscular Contraction in Man. J. Physiol., 57: p. 68, 1922.

55. Macherson, L., A Method of Determining the Force-Velocity Relation From Two Isometric Contractions. J. Physiol., 122: p. 172, 1953.

56. Marisi, D. Q., The Genetic Component in Motor Performance and Numeric Memory. Unpublished Doctor's Dissertation, University of California, Berkeley, 1972.

57. McNemar, Q., Twin Resemblances in Motor Skills and the Effect of Practice Thereon. J. of Genetic Psychol., 42: p. 70, 1933.

58. Mowrer, E. R., Some Factors in the Affectional Adjustment of Twins. Amer. Sociological Review, 19: p. 468, 1954.

59. Newman, H. H., F. N. Freeman, and K. J. Holzinger. Twins - A Study of Heredity and Environment. The University of Chicago Press, 1937.

60. Osborne, R. H., and F. V. Degeorge. Genetic Bases of Morphological Variation. Harvard University Press, Cambridge, Mass., p. 17, 1959.

61. Partanen, J., K. Bruun, and T. Markkanen. Inheritance of Drinking Behavior. A Study of Intelligence, Personality and Use of Alcohol of Adult Twins. The Finnish Foundation of Alcohol Studies, Helsinki, 1966.

62. Pavan, C., and R. Basile. Chromozome Changes Induced by Infections in Tissues of Rhynchosciara angelae. Science, 151: p. 1556, 1966.

63. Portenier, L., Twinning as a Factor Influencing Personality. J. Educational Psychol., 30: p. 592, 1939.

64. Price, B., Primary Biasis in Twin Studies; a Review of Prenatal and Natal Differences - Producing Factors in MZ Pairs. Amer. J. Human Genetics, 2: No. 4, p. 293, 1950.

65. Ralston, H. J., M. J. Polissar, V. T. Inman, J. R. Close, and B. Feinstein. Dynamic Features of Human Isolated Muscle in Isometric and Free Contractions. J. Appl. Physiol. 1: p. 526, 1949.

66. Ritchie, J. M., and D. R. Wilkie. The Dynamics of Muscular Contraction. J. Physiol., 143: p. 104, 1958.

67. Robinson, S., Experimental Studies of Physical Fitness in Relation to Age. Int. Angew Physiol., 10: p. 251, 1938.

68. Sank, D., Genetic Aspects of Early Total Deafness. In Family and Mental Health Problems ~~in a Deaf~~ Population, ~~New York~~. New York State Psychiatric Institute, p. 28, 1963.

69. Sargent, F., and K. P. Weinman. Physiological Individuality. Ann. New York Acad. Sci., 134: p. 696, 1966.

70. Schoenfeldt, L. F., A Comparison of Two Analytic Procedures for Estimating Twin Zygosity. Human Heredity, 19: p. 343, 1969.

71. Shield, J., Monozygotic Twins Brought Up Together; an Investigation into the Genetic and Environmental Causes of Variation in Personality. London Oxford University Press. Toronto, 1962.

72. Sonnenblick, E. H., Implications of Muscle Mechanics in the Heart. Federation Proc., 21: p. 975, 1962.

73. Stevens, H. C., and R. P. Metcalf. The Decrement in Muscular Force with Increasing Speed of Shortening. Amer. J. Physiol., 107: p. 568, 1934.

74. Stevens, H. C., and J. M. Snodgrass. A Quantitative Study of the Changes in Power During Muscular Contraction. Amer. J. Physiol. 104: p. 276, 1933.

75. Storrs, E. E., and R. J. Williams. A Study of Monozygotic Armadillos in Relation to Mammalian Inheritance. Proc. National Acad. Sci., United Stated, 60: p. 910, 1968.

76. Sutton, H. E., S. G. Vandenberg, and P. J. Clark. The Hereditary Abilities Study: Selection of Twins; Diagnosis of Zygosity and Program of Measurements. Amer. J. Human Genetics. 14: p. 52, 1962.

77. Vandenberg, S. G., Contributions of Twin Research to Psychology. Psychol. Bull., 66: p. 327, 1966.

78. Vandenberg, S. G., The Hereditary Abilities Study: Hereditary Components in a Psychological Test Battery. Amer. J. of Human Genetics, 14: p. 220, 1962.

79. Vandenberg, S. G., Heritability Estimates of Anatomical Measurements in Man. In Biological Handbook on Growth. Washington, D.C., Federation of American Societies for Experimental Biology, p. 110, 1962.

80. Vandenberg, S. G., How Stable are Heritability Estimates? A Comparison of 6 Anthropometric Studies. Amer. J. Physical Anthropology, 20: p. 331, 1962.

81. Vandenberg, S. G., Innate Abilities, One or Many? A New Method and Some Results. Acta.Genet. Med. Gemellol., 14: p. 41, 1965.

82. Vandenberg, S. G., P. J. Clark, and I. Samuels. Psychophysiological Reactions of Twins: Heritability Estimates of Galvanic Skin Resistance, Heart Beat, and Breathing Rates. Eugenics Quarterly, 12: p. 7, 1965.

83. Weber, G., W. Kartodihardjo, and V. Klissouras. Growth and Training: A Co-Twin Study. Unpublished work and personal communication, 1973.

84. Whittinghill, M., Human Genetics and its Foundations. Reinhold Publishing Corporation, New York, 1965.

85. Wilkie, D. R., The Relation Between Force and Velocity in Human Muscle. J. Physiol., 110: p. 249, 1949.

86. Wilson, P. T., A Study of Twins with Special Reference to Heredity as a Factor Determining Differences in Environment. Human Biology, 6: p. 324, 1934.

APPENDIX A

SUBJECTIVE CRITERIA

PHYSICAL METHOD OF CLASSIFICATION

TWIN	Hair Colour	Hair Texture	Eye Colour	Iris Pattern	Ear Lobe	Nose	Ht.	Wt.

COMMENTS

INTERVIEW

Family Background

Leisure Activities

Physical Activities

COMMENTS (Rough Diagnosis)

MEDICAL EXAMINATION

NAME: ______________________________

CHEST: ______________________________

____

____

HEART: Rate Blood Pressure Sounds

____

____

ECG ______________________________

OTHER: ______________________________

____

____

____

COMMENTS:

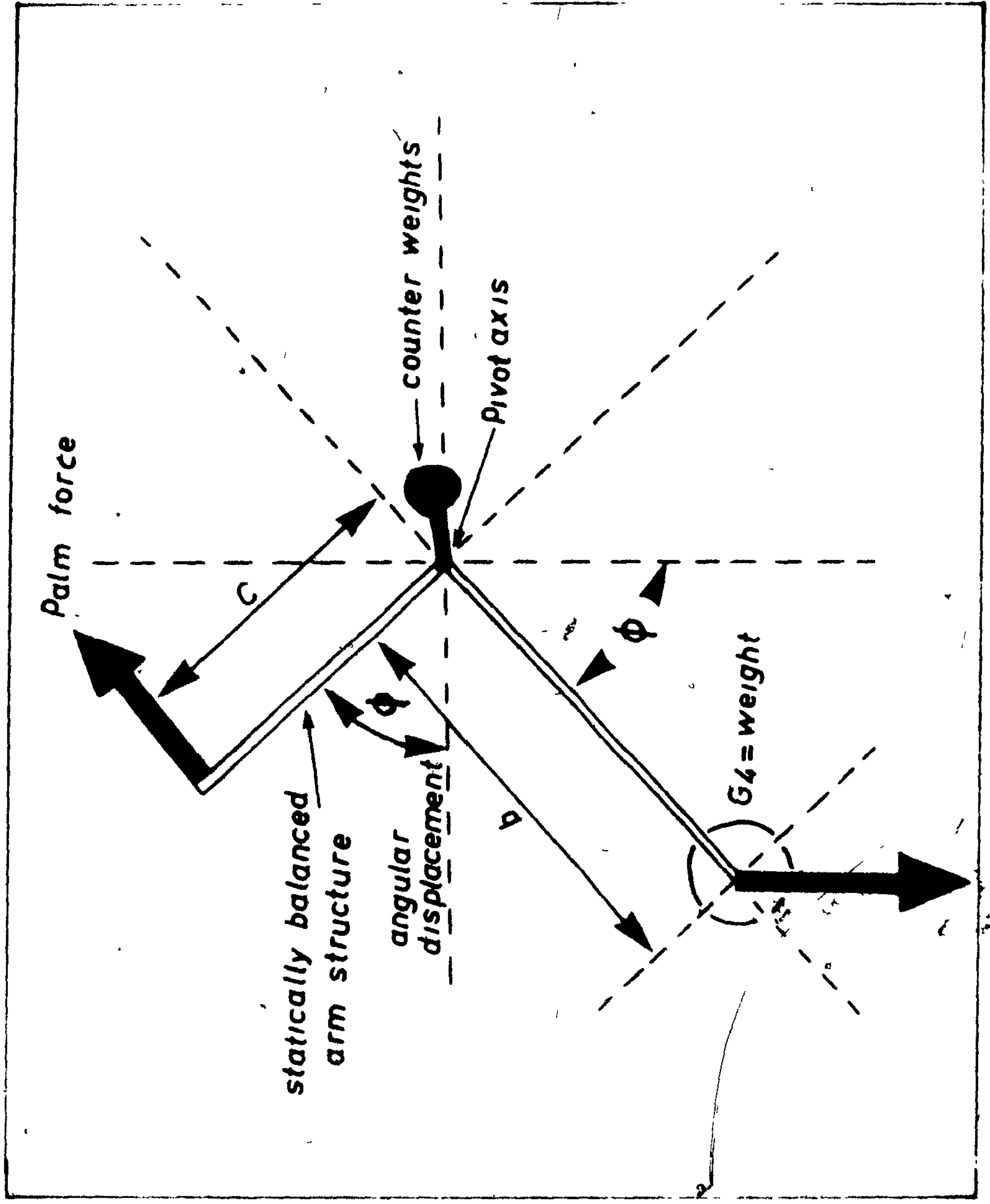
DATE: ____________________ ____________________

Signature of Examiner

APPENDIX B

DERIVATION OF FORMULA

Figure 22:- Conceptual Arrangement of the Ergometer



Derivation of Palm Force

Using the conceptual arrangement (Figure 22), the dynamic balance of the system can be represented by:

$$F_p.C.\text{Sine}\,\phi = (G_4.b.\text{Sine}\,\phi + I_s)\ddot{\phi} \qquad \text{(XII)}$$

where:

F_p = the dynamic palm-force (kg) acting perpendicular to the arm of the machine

C = distance (cm) between the pivot axis and the point of application of the palm-force

G_4 = the weight of the "weight" (3.2, 6.5 or 9 Kg) on the resistance arm of the ergometer

ϕ = the angular displacement (degrees) of the human arm with respect to the horizontal

I_s = the resultant moment of inertia of the system as defined by Equation XIII below

b = the distance between the pivot axis and the center of gravity of the weight. By the geometry and construction of the machine b=69.4-0.0.0232 x r, where r = the reading on a numerical counter which determines b distance

$\ddot{\phi}$ = the second derivative of ϕ with respect to time (angular acceleration). Note that it can be positive, negative, or zero. It is positive if the arm is accelerated, negative if the arm is decelerated, and zero if the arm is either stationary or moves with a constant angular velocity.

The resultant moment of inertia of the system (I_s) about the pivot axis is:

$$I_s = \frac{G_4.b^2}{g} + I_2 + I_3 \qquad \text{(XIII)}$$

where:

I_s = as defined above

G_4 = as defined above

b = as defined above

g = the constant of gravitational acceleration (981 cm/sec^2)

I_2 = the moment of inertia of the human forearm with respect to the pivot axis

I_3 = the moment of inertia of the frame structure of the ergometer with respect to the pivot axis

Therefore, by Equations XII and XIII, the total palm-force can be represented by:

$$F_p = \frac{G_4 . b . \text{Sine}\,\Phi}{C} + \left[\left(\frac{G_4 . b^2}{g} + I_2 + I_3\right)\ddot{\Phi}\right] / C \qquad \text{(XIV)}$$

In Equation XIV, the total palm-force is the summation of two components, the static plam force necessary to hold the load (G_4) and the dynamic palm force necessary to produce a given angular acceleration ($\ddot{\Phi}$). The angular acceleration ($\ddot{\Phi}$) becomes zero when the angular velocity of the lever arm of the ergometer moved with a constant angular velocity. This was found to occur within the angular range of 80 to 90 degrees and hence, all force measurements were made at an angle of 85 degrees with respect to the horizontal. Consequently, Equation XIV was reduced to its static component and forces were calculated from the Equation XI that previously was presented.

$$F_p = \frac{G_4 . b . \text{Sine}\,\Phi}{C}$$