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THE EFFECTS OF DENERVATION AND TRAINING ON THE PROPERTIES OF LINEAR AND NON-LINEAR MECHANICAL MODELS OF RAT GASTROCNEMIUS

by

Peter Thomas Harrower
BSc (Kines.), Simon Fraser University, 1973

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
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Degree: Master of Science (Kinesiology)

Title of Thesis: The Effects of Denervation and Training on The Properties of Linear and Non-Linear Mechanical Models of Rat Gastrocnemius

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Author.

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PETER T. HARROWER

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Aug. 23/76

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ABSTRACT

A number of models of muscle have been developed with the expressed purpose of revealing internal events occurring in muscular subunits during contraction. In 1950, Hill developed a model of muscle which comprised a contractile component and a series elastic component with another elastic component in parallel. Although the properties of this model and of muscle are non-linear, there have been recent attempts at development of a linear model which can adequately represent the muscle since a linear approximation simplifies manipulation of data and reduces the number of repeated muscular contractions require for analysis. To date, most investigators have been concerned with the mechanical properties of a single model of muscle determined under either dynamic or isometric conditions and little effort has been made to describe or compare the properties of the linear and non-linear models of muscle obtained during isometric contractions. Furthermore, a comparison of these models has not been performed for a variety of abnormal conditions of muscle. The effects of disease, injury and drugs on the structure of muscle have been investigated by histological, histochemical and biochemical techniques. Although the observed structural changes associated with these conditions have beem assumed to have an effect on the mechanical properties of muscle, structural and mechanical changes in each of the components of muscle have not been examined simultaneously.

The present study was designed to determine the effects of denervation and training on the properties of a linear and non-linear model of muscle during isometric contraction. Initially, attention was directed towards assessing and comparing the mechanical properties of both models during a rise in isometric force. In addition, muscle tissue from one

denervated and one sedentary rat were examined by histological and histochemical techniques in order to determine the relationship between structural changes and the mechanical properties during isometric contraction.

Denervation and training affected the mechanical properties of muscle as interpreted by both models. The magnitude of the force-velocity relationship of the contractile components was significantly reduced by prolonged denervation. This reduction was demonstrated by a significant decrease in the maximal force production (97.3%) and maximal velocity (99%) attained during isometric contraction. Training produced an increase of approximately 40% in the maximal velocity of shortening of the contractile component. There was found to be no significant change in the maximal force produced by the contractile component due to training. Prolonged denervation increased the compliance of the series elastic component over the full range of isometric force whereas training increased compliance only at lower levels of force. The parallel elastic component became stiffer as a result of denervation, training and prolonged disuse. When comparison was made between the linear and non-linear parameters of the above relationships, it was suggested that the linear model produced greater changes (approximately 20%) than were observed in the non-linear model. This result was thought to be a consequence of one of the basic assumptions inherent in the linear model.. It was shown that the mechanical properties present in isometric contractions were different from those reported for dynamic contractions. The present results yielded low values of velocity in low regions of force whereas dynamic contractions yield high values in the same regions of force. This phenomenon was attributed to the assumption that active state develops as the isometric contraction progresses. Furthermore, there was a direct correlation between

structural changes and the mechanical properties of the denervated rat gastrocnemius.

ACKNOWLEDGEMENT

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CHAPTER I

INTRODUCTION

The mechanical properties of striated muscle are commonly described with reference to a three component model (Hill, 1950). This model comprises an actively contracting component (CC) in series with a passive elastic component (SEC), both being in parallel with another passive elastic component (PEC). This model has been used to simulate dynamic muscular contraction.

A.V. Hill (1938) suggested that the isometric myogram is uniquely determined by the force-velocity relationship of the CC and the stress-strain relationship of the SEC. This suggestion has been experimentally applied without its verification by Katz (1939), Hill (1949) and Wilkie (1950) who assumed that the force-velocity relationship determined dynamically was the same as that determined under isometric conditions. MacPherson (1953) produced results which appeared to substantiate this assumption. However, the isometric and dynamic experiments performed by Parmley, Yeatman and Sonnenblick (1970) demonstrated that the force-velocity relationship of the CC determined from isometric contractions is distinctly different from that obtained during dynamic contractions. While numerous studies have been performed which support the results of Parmley et al. (1970), little direct experimentation has been conducted to determine whether the mechanical properties of the SEC vary between dynamic and isometric contractions as does the force-velocity relationship of the CC.

Following Hill's (1950) work, a number of models of increasing complexity have been developed to account for the variety of information

obtained on the separate mechanical components. As models of muscle have increased in complexity to encompass the whole neuromuscular control system, some efforts have been made at simplification in order to facilitate analysis. One such model was presented by Houk (1963) who used linear approximations of the non-linear mechanical properties of the components in Hill's model which simplified the simulation of these properties while being sufficiently accurate. Linearization was performed on the mechanical properties of the CC and SEC obtained during dynamic contractions. When these linear properties were used to deduce an isometric myogram the latter fitted that experimentally produced. On this basis Houk (1963) assumed the validity of the process of linearization. However the application of dynamic properties in an isometric condition are subject to question.

A great deal of histological, histochemical and biochemical information has been acquired concerning the effects of denervation and training on the structure of striated muscle. Such results have led investigators to draw conclusions on the effects of denervation and training on the mechanical properties of the musculo-tendinous system. To date, little direct research has been performed which has allowed comparison of measured mechanical properties with mechanical properties deduced from observed structural changes.

The purpose of this study was fourfold. The initial aim was to describe the properties, obtained during isometric contraction, of components of both the linear and non-linear models of muscle. The second aim was to describe the changes in these properties which were the result of denervation and training. Thirdly, the changes in the linear and non-linear properties, brought about by denervation and

training, were compared in an attempt to determine whether each model is equally useful for revealing changes in the musculo-tendinous system. A fourth aim was to explain changes in the mechanical properties by recourse to structural information.

It was hoped that the results of this investigation would provide a complete dossier of information concerning the mechanical properties of muscle during isometric contraction along with the effects of some experimental treatments on these properties of mammalian skeletal muscle. This information should have application in the fields of Physical Medicine, Physical Eduation and Rehabilitation.

CHAPTER II

REVIEW OF RELATED LITERATURE

A. BIOMECHANICS OF SKELETAL MUSCLE

The mechanical behavior of skeletal muscle has been explained by a mechanical model comprising three functionally different components (Hill, 1950). The contractile component (CC) was considered to be in series with an elastic component (SEC), both being in parallel with another elastic component (PEC). This type of representation has been accepted as a good approximation of the actual muscular system under certain experimental conditions.

Hill (1938) suggested that during isometric contraction the CC of the muscle shortens at the expense of the SEC. He concluded that the form of the isometric myogram is uniquely determined by the force-velocity (F/V) curve of the CC and the stress-strain (E/F) curve of the SEC as follows:

$$\frac{dP}{dt} = \frac{dP}{dx} \cdot \frac{dx}{dt} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (1)$$

where P = force produced

x = the length of the SEC

t = time

This relationship is applicable to those isometric contractions which are perfomed at a muscle length where the contribution to tension by the PEC can be neglected (Bahler, 1967). It was found that when the isometric length was greater than the resting length (Lo) the effects of the PEC could be subtracted from the total output of force because the PEC developed a passive force which is constant at any given length. Therefore, as Hill (1938) suggested, investigators are concerned only with two of the

three components of the muscle model when considering isometric contractions at any muscle length after compensating for the effects of the PEC.

In passive conditions the CC is thought to be very compliant and any resting tension, which increases exponentially with increased lengths, is considered to be due to the PEC (Hill, 1950; Wilkie, 1956; Jewell and Wilkie, 1958). In dynamic conditions the total tension produced is the sum of tension due to active contraction of the CC and that due to the PEC. In such conditions the force developed by the CC is thought to be uniquely related to the velocity of shortening by the hyperbolic F/V relationship (Hill, 1950; Wilkie, 1950, 1956; Sonnenblick, 1964).

i) The force-Velocity Relationship of the Active Contractile Component

The velocity of shortening of active isolated muscle has long been known to be inversely related to the magnitude of the load lifted (Fick, 1893; Blix, 1898; Levin and Wyman, 1927; Fenn and Marsh, 1935; Wilkie, 1950; Jewell and Wilkie, 1958).

Levin and Wyman (1927) developed an ergometer which permitted the muscle to shorten at a constant velocity. They confirmed that the force produced by the muscle diminished as the velocity of the shortening of the CC increased. Therefore the maximal force was developed when the velocity of shortening was zero (ie., isometric contraction). Fenn and Marsh (1935) verified these finding using isotonic contractions (shortening when tension is contant). They initiated their research under the supposition that the muscle consisted of two springs in series, one being undamped and non-contractile while the other was embedded in a viscous medium. Under these conditons a linear F/V relationship was expected. Yet they found in isolated muscle of both the frog and cat that the

relationship was convex towards the origin and it was described by the following exponential equation:

$$P = P_o e^{-aV} - K.V \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (2)$$

where a and K were constants, P was the force generated, P_o was the force produced isometrically and V was equal to the velocity of the shortening of the CC.

A similar relationship was found by Hill (1938), who suggested that the shape of the F/V relationship was governed by the way in which energy was released during muscle shortening. He produced the following equation from thermal measurements which fitted both the mechanical data of Fenn and Marsh (1935) and subsequent results by other investigators (Katz, 1939; Wilkie, 1950; Jewell and Wilkie, 1958; Thompson, 1961):

$$(P + a)\ (v + b) = c = (P_o + a)b \quad . \quad . \quad . \quad . \quad . \quad . \quad (3)$$

where a, b and c are constants,

v = v = velocity of shortening,

P = force of contraction and

P_o = the isometric force produced

These findings resulted in the "classic" F/V relationship which has been accepted by most authors as indicative of the mechanical properties of the CC under dynamic conditions (FIGURE 1).

Bahler, Fales and Zierler (1968) extended the work of Hill and found that a family of F/V curves existed, each curve being dependent upon the length either from which shortening began or at which measurements were taken. These authors concluded that there was a complicated inter-relationship between velocity of shortening, muscle length and force which

must be investigated in order to understand fully the functional properties of the CC (FIGURE 2a). Although it was found that there were definite changes in magnitude of force and velocity at various lengths, which were partially indicated by the static force-length relationship of the CC, the general hypobolic shape of the F/V curve did not change for different lengths (Bahler et al., 1968). That is, these curves were found to be approximately parallel (FIGURE 2a). Thus, the CC can best be described as that element of the muscle responsible for the length, velocity and force relationship when the effects of the SEC are removed.

The "classic" F/V relationship was developed through the use of dynamic and isotonic conditions which represent actual external shortenings of the muscle. Parmley, Yeatman and Sonnenblick (1970) indicated that the F/V relationship acquired under isometric conditions was quite different from the "classic" relationship developed under dynamic conditions. They determined that the velocity of shortening of the CC at any given load was lower during isometric contractions than during isotonic contractions. Furthermore, they indicated a rapid rise in the velocity of the CC at low forces which reached a peak value then decreased as the force increased. When the peak value was reached the form of the F/V curve followed the same concave to origin pattern as the classic curve, but at a reduced level of velocity for any given force. Parmley et al. (1970) summarized

> that during the early isometric portion of contraction a rising active state which would increase the CC velocity is more than balanced by the increase in force and a reduction in the CC length, both of which would reduce CC velocity. The net result during this phase of contraction is a constant reduction in the CC velocity following

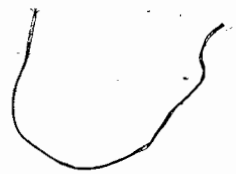


FIGURE 1:

The classic force-velocity relationship of the contractile component of muscle at L_o.

(Jewell and Wilkie, 1958; p. 521)

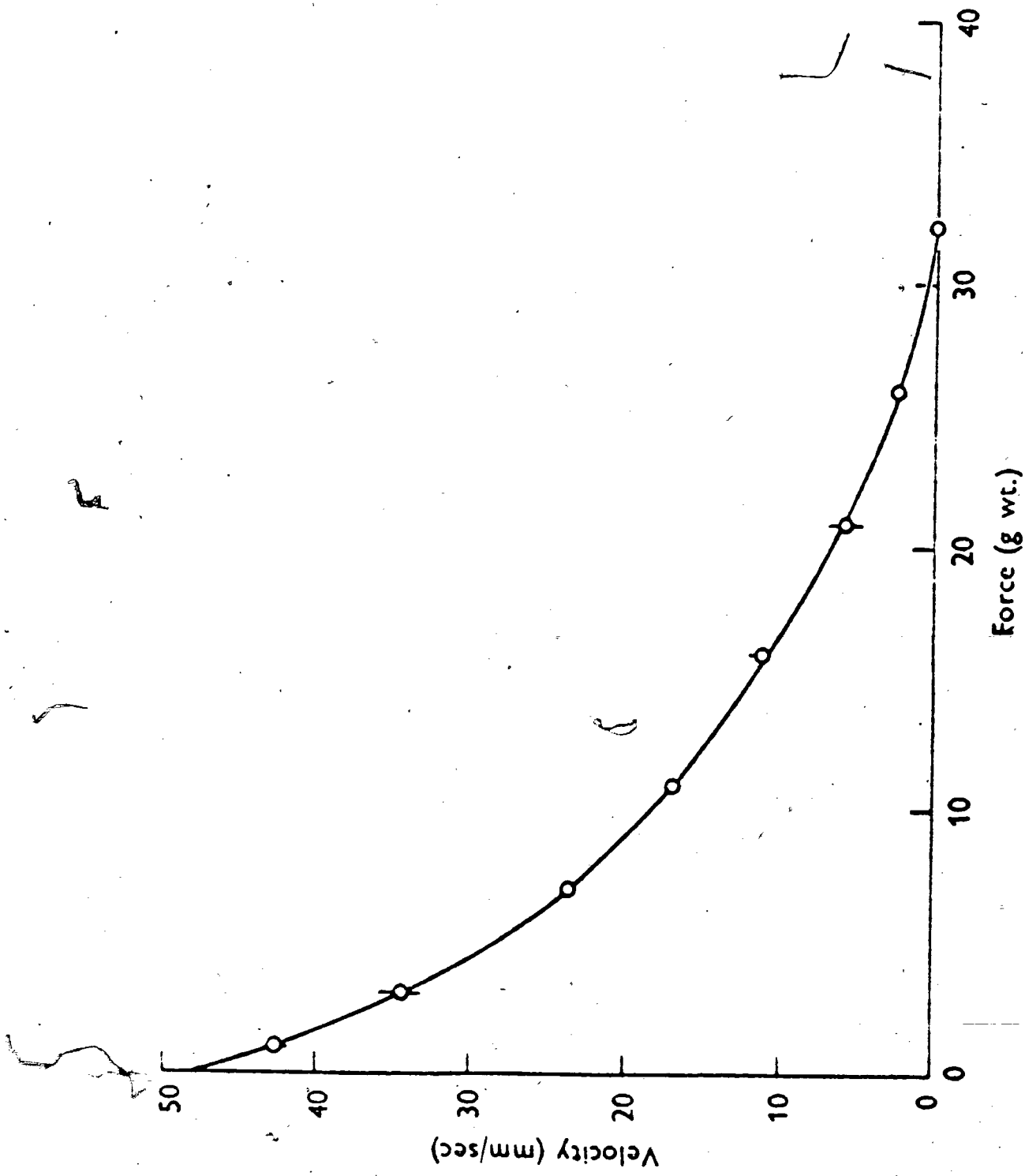
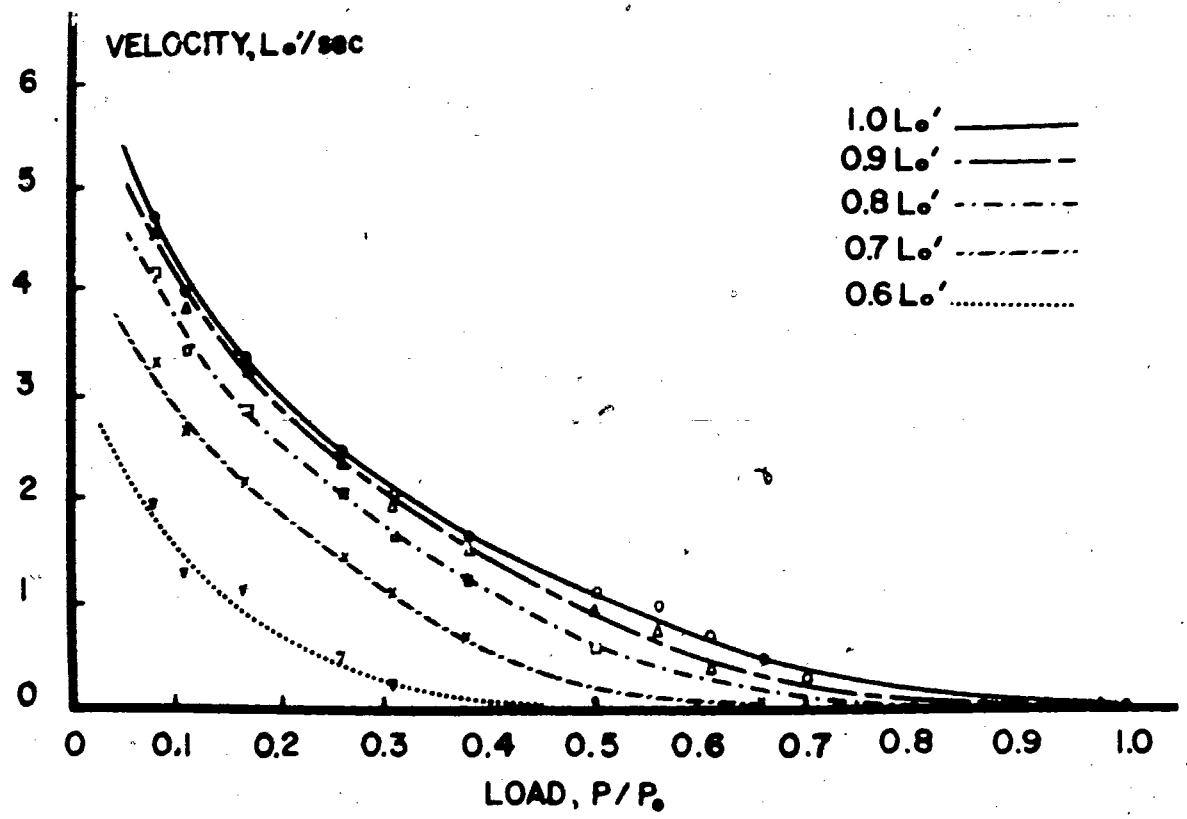

Velocity (mm/sec)
0
10
20
30
40
50
Force (g wt.)
0
10
20
30
40

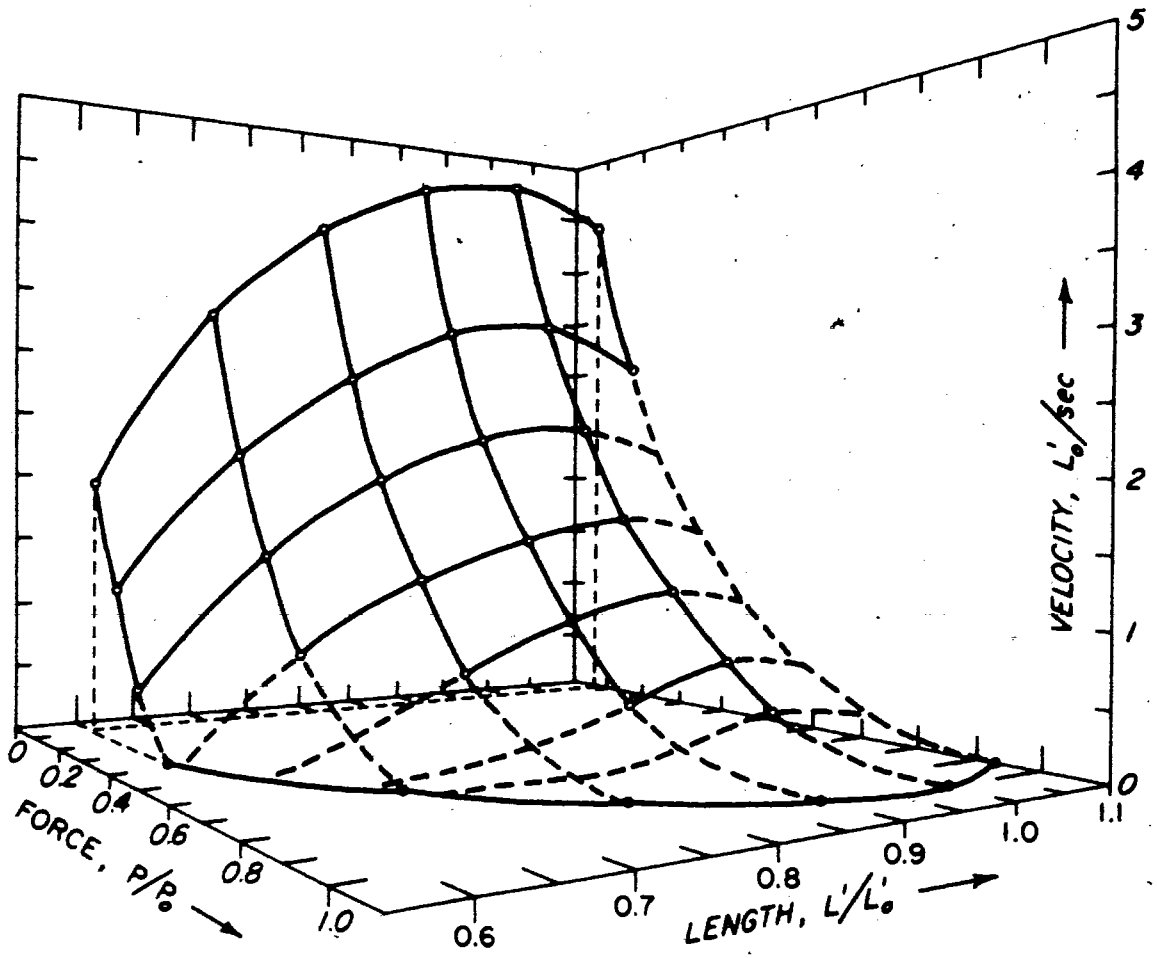
FIGURE 2:

a) Normalized isotonic force-velocity curves of the contractile component at various lengths of the contractile component (p. 376).

b) Three-dimensional representation of the dynamic length-force-velocity phase space of the contractile component (p. 377).

(Bahler, Fales and Zierler, 1968)


VELOCITY, Lo'/sec
6
5
4
3
2
1
0
1.0 Lo'
0.9 Lo'
0.8 Lo'
0.7 Lo'
0.6 Lo'
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
LOAD, P/Po


5
4
3
2
1
0
VELOCITY, Lo'/sec
0
0.2
0.4
0.6
0.8
1.0
FORCE, P/Po
0.6
0.7
0.8
0.9
1.0
1.1
LENGTH, L'/Lo'

> an initial early peak. As the afterload is reached and lifted, CC velocity rises, presumably because of the influence of a rising length, since force is no longer rising.
>
> (Parmley, Yeatman and Sonnenblick, 1970; p. 550)

The above authors concluded that there exists a distinct difference between the F/V curves derived from dynamic conditions and those derived from isometric conditions by application of equation (1).

The F/V relationship of the CC has been determined from data obtained by use of a technique involving the addition of an added compliance in series with the muscle during isometric contractions. This technique was first developed by MacPherson (1953) who showed that from a single pair of isometric contractions, one without and one with an added series compliance, the E/F relation of the SEC and the F/V curve of the CC could be derieved. The sole assumption made was that the velocity of shortening at any moment was a function only of the force at that moment. Parmley and Chuck (1973) studied the mechanical effects of an added compliance placed in series with the muscle, on both the maximal force output and the subsequent calculated F/V relationship during isometric contractions. Their results indicated a reduction in the maximal force (P_o) in these contractions that incorporated the added series compliance. They concluded that the observed reduction in P_o was directly related to the compliance of the spring placed in series. This indicated that the reduced maximal force was due to the muscle shortening to a length which was less than the muscle length presen during the isometric contractions incorporating no added compliance.

The observation by Parmely and Chuck (1973) that the reduced P_o

obtained when a spring was added in series was not indicated in MacPherson's research. In fact, MacPherson's system of analysis required a pair of isometric contractions with the same terminating magnitude of force. As Parmley and Chuck (1973) concluded, the discrepancy between these findings was due to the compliance of the springs used in the separate experiments. This conclusion was confirmed by comparing the spring compliances used by both MacPherson and Parmley et al., where MacPherson used a spring whose compliance was approximately 50 times less. Thus, the discrepancy in maximal force production shown by Parmley and Chuck (1973) was due to the high extensibility of the added series compliance which resulted in a large change in the length of the CC.

An alternative method of analyzing muscle contractions was presented by Houk (1963). He suggested that a viscoelastic model which assumed linear approximations for both the F/V relationship of the CC and the E/F relation of the SEC would be acceptable. Houk reasoned that the adoption of linearized approximations would simplify the simulation of the mechanical properties of muscle. This linear model was designed to demonstrate the mechanical properties of dynamic contractions and thus, the classic F/V relationship of the CC. To date, the responses of this linear model have not been evaluated under isometric contractions but it is probable that this model could be adopted to analyze isometric contractions by incorporation of the added series compliances technique developed by MacPherson (1953).

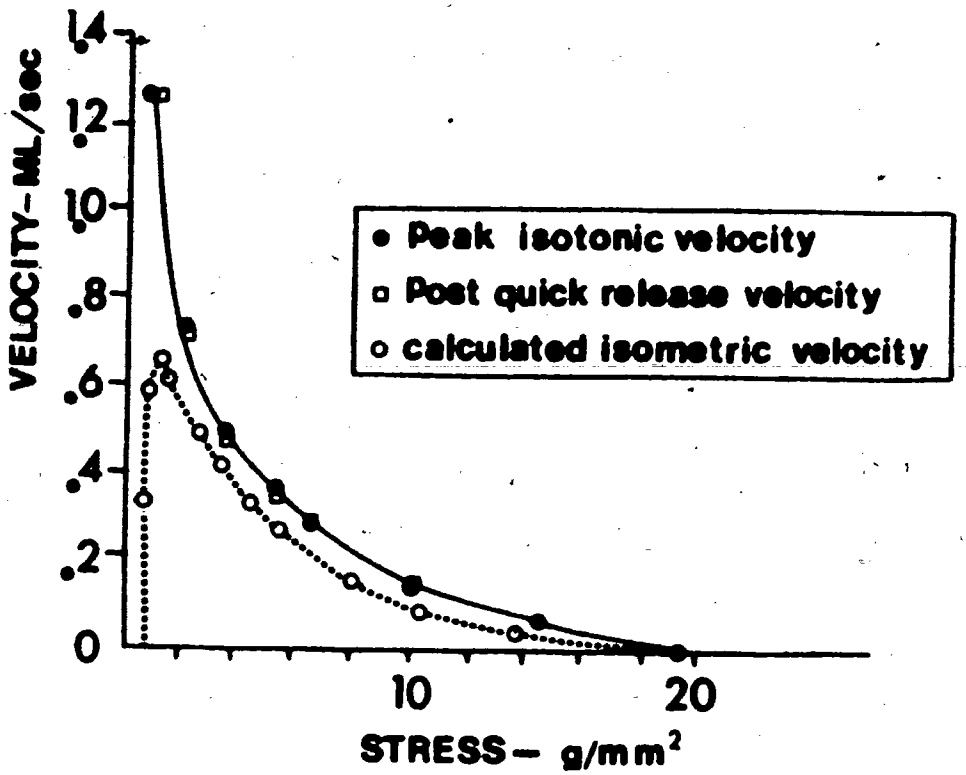
ii) The Stress-Strain Relationip of the Series Elastic Component

According to Hill (1938), during isometric contraction the CC shortens at the expense of the SEC and therefore the force is developed across the SEC in accordance with its E/F characteristics.

FIGURE 3:

Comparative force-velocity relations of the contractile component obtained from isotonic (●), quick release (◘), and isometric (○) contractions.

(Parmley, Yeatman and Sonnenblick, 1970; p. 548)


VELOCITY-ML/sec
1.4
1.2
1.0
.8
.6
.4
.2
0
10
20
STRESS— g/mm²
• Peak isotonic velocity
□ Post quick release velocity
○ calculated isometric velocity

The existence of an elastic component in series with the CC is deduced primarily on the biphasic response of a muscle during quick release (Wilkie, 1956; Jewell and Wilkie, 1958; Bahler, 1967; Bahler et al., 1968; Cavagna, 1970; Close, 1972). When the muscle is released during isometric contraction and allowed to shorten against a load less than the isometric tension, it exhibits an initial rapid phase of shortening which is completed within a few milliseconds (Close, 1972). This initial phase was attributed to the release of elastic energy stored in the SEC after the change in load. The second, slower phase is thought to be the result of shortening of the CC in accordance with its F/V properties (Jewell and Wilkie, 1958). Due to this biphasic response to quick release experiments it was concluded that the SEC was the component of the muscle which reacts to a instantaneous decrement of load.

Structurally, the force generated by the CC has been widely assumed to be the result of cross-bridge formation between the actin and myosin filaments (Podolsky, 1960). The SEC presents a much more difficult problem in the determination of structural sites. Jewell and Wilkie (1958) concluded that half of the series compliance resided in the tendon with the remainder being distributed along the muscle fibres. These observations had been accepted up until 1971, when Huxley and Simmons (1971a) presented convincing evidence to the contrary.

Huxley and Simmons (1971a) suggested that the greater part of the muscle's series elastic compliance appears to reside in the sarcomere with the majority being in the cross-bridges themselves. These findings have been duplicated recently by Bressler and Clinch (1974). Both groups of investigators questioned whether or not the tendon contributed to the muscle's series compliance in a prominent way. They suggested that if

most of the muscle's series compliance resided in the tendon then at increasing lengths the muscle's series compliance should decrease, thus indicating its independence of contractile activity. On the contrary, these authors found an increase in the muscle's series compliance at muscle lengths greater than Lo thereby demonstrating a direct relationship between contractile activity due to numbers of available cross-bridges and the muscle's series compliance (Huxley and Simmons, 1971a; Blange, 1972; Bressler and Clinch, 1974; Grood, 1975). Furthermore, they found the increased muscle compliance corresponded to a decreased area of overlap of the myofilaments and thus a decrease in the number of force generating cross-bridges (Gordon, Huxley and Julian, 1966). Bressler and Clinch (1974) concluded that a muscle's compliance was closely related to its contractile activity or more specifically, to the contractile activity of the cross-bridges. These studies succeeded in disproving a popular misconception of a major contribution of tendon to the properties of the SEC.

It was suggested that part of the SEC residing in the sarcomeres consisted of two components. The first was a passive elastic component which was in series with the elasticity of the cross-bridges. The latter was represented by a parallel combination of a spring and dashpot (Huxley and Simmons, 1971a). The results obtained by Huxley and Simmons (1971a), and Bressler and Clinch (1974) indicated a direct relationship between the numbers of active cross-bridges, area of overlap of the myofilaments, and the SEC compliance. Therefore, it was concluded that most of the muscle's series compliance was length dependent. An added suggestion made by Huxley and Simmons (1971a) indicated that the portion of the SEC that resided in the cross-bridges was also time dependent.

Katz (1939), Hill (1949) and Wilkie (1950) determined that the SEC of frog muscle was stretched 6 - 10% of the total muscle length at full isometric tension. At that time these figures were consistent with those found earlier by Gasser and Hill (1942). Jewell and Wilkie (1958) indicated that these findings were considerably greater than the actual values. In fact, Hill (1950, 1953) estimated that these values were twice as large as those found by direct measurement. Jewell and Wilkie (1958) suggested that the actual figure for the muscle's series compliance at maximum isometric tension was closer to 3% for frog muscle.

Conflicting results for total compliance arise when comparing the SEC's of different animals. Sonneblick (1964) determined that for cat papillary muscle the SEC was stretched 8 - 10% of the initial muscle length during isometric force generation. He concluded, as did Abbott and Mommaerts (1959), that the SEC of papillary muscle was considerably more compliant than skeletal muscle of the same animal. Whereas Jewell and Wilkie (1958) summarized total series compliance of 3% for frog skeletal muscle, Bahler (1967) found that there was a maximum extension of the SEC of 7% for rat gracilis anticus muscle. Close (1972) concluded these differences were due, probably, to differences in the amount of series connective tissue in the muscles and to variations in the elastic properties of these tissue and structures within the muscle fibres themselves.

Evidence presented by Close (1972) suggested that the extension of the SEC at maximum isometric tension varied little between skeletal muscles of the same animal. This was found to be consistent with the results reported by Hill (1950, 1953), Jewell and Wilkie (1958) and Cavagna (1970). In these studies the extension of the SEC was determined

to be 2 - 3% of the initial muscle length of the soleus sartorius and gastrocnemius of the frog. Data presented by Close (1972) concerning rat skeletal muscle lent further support to this suggestion. In fact, the estimates he presented indicated an extension of 6 - 7% for cat gracilis anticus, soleus and tibialis anterior. Close (1972) indicated that these figures were higher for measurements in vitro than those in situ, but stated that the figures were consistent from muscle to muscle in each situation. He suggested that the differences were partly due to the damping effect of surrounding tissue in situ.

In all the studies mentioned, at least one of the following techniques was used to calculate the E/F curve of the SEC:

1) the controlled release method using fast constant velocity releases (Hill, 1950),
2) the quick release method where the force across the muscle is changed from isometric to a given isotonic level (Wilkie, 1956; Jewell and Wilkie, 1958),
3) calculation of the E/F curve from the force-time relations for isotonic shortening and isometric tension development (Hill, 1938), and
4) calculating the compliance-force (C/F) and E/F curves from only two isometric contractions, where one contraction is without and the other with an added compliance in series with the muscle (MacPherson, 1953; Houk, 1963; Parmley et al., 1970, 1973).

Methods 1) and 2) are direct measurement techniques, while 3) and 4) are calculated or estimated methods of determining the compliance of the SEC. Discrepancies in the corresponding F/V relation of the CC

have been found between these two types of techniques. Parmley et al. (1970) concluded that part of the discrepancy between the two techniques was due to the use of isotonic and isometric contractions in the direct and calculated techniques respectively. Very little evidence has been presented to indicate any difference in the resulting E/F curves of the two techniques.

The validity of Hill's (1958) model has been tested by comparing the observed and calculated values for the three variables presented in equation (1). Katz (1939) and Jewell and Wilkie (1958) experimented on frog muscles and found that the estimated values of rate-of-rise of tension $\frac{dP}{dt}$ in isometric contraction were higher than the observed values. MacPherson (1953), Parmley et al. (1970) and Parmley and Chuck (1973) found that the calculated speed of shortening $\frac{dx}{dt}$ of the CC of rat soleus muscle was less than that observed during isotonic contractions. The estimated compliance of the SEC $\frac{dx}{dP}$ of cat tenuissimus muscle was found to be twice that obtained by the direct controlled release method (McCrorey, Gale and Alpert, 1966). These discrepancies have not been satisfactorily explained as yet. Close (1972) suggested one possibility which might account for part of the difference. He stated that at particular loads and lengths, the velocity of shortening of the CC as a whole may be less in isometric than in isotonic contractions and that this may have been the result of the rising activation state in the muscle. Parmley et al. (1970) made a similar suggestion when they examined the isometric F/V relationship. They showed an almost instantaneous increase in the velocity of shortening of the CC during the transition from isometric to isotonic contraction, where the maximum velocity of shortening was reached much later in the contraction. These findings were supported by Bahler

et al. (1968) who concluded that after a period of acceleration the peak isotonic shortening velocity which occurred was larger than that found for isometric conditons. Close (1972) concluded from these accumulated results that there would be a higher recording of compliance of the SEC $\frac{dx}{dP}$ and an increased rate of tension development $\frac{dP}{dt}$ in the isometric conditons (equation 1). Furthermore, Close (1972) suggested that the effects of both transition from one type of contraction to another and the previous mechanical activity on another contraction were difficult to assess due to insufficient quantitative information. But he did not discount that these factors may have partially accounted for the discrepancy found.

Earlier investigations have produced the E/F relationship of the SEC for a number of different animals and muscles using the quick release or controlled release techniques (Wilkie, 1950, 1956; Ritchie and Wilkie, 1958; Jewell and Wilkie, 1958; Sonnenblick, 1964; Bahler, 1967; Bahler et al., 1968; Parmley et al., 1970; Bressler and Clinch, 1974). In each of these studies dynamic contractions were examined and the resulting E/F relationships were similar in shape. Characteristically, the E/F relationship of the SEC was represented by large increases in the length of the SEC as force increased; but as force approached a maximum, the length changes of the SEC became smaller (FIGURE 4). Through the years this general shape for the E/F relationship has been accepted as a description of the mechanical behavior of muscle's SEC during muscle activation.

MacPherson (1953) determined the F/V relationship of the CC and the E/F relation of the SEC using a technique involving only two isometric contractions. Parmley et al. (1970) indicated that MacPherson had seemingly

ignored the initial points, representing low velocity and low force, of his F/V data. Parmley et al. (1970) suggested that his oversight was probably due to biased expectations and therefore the E/F relationship produced from this data was also suspected to be biased in its agreement with that obtained by direct measurement of dynamic contractions. To alleviate this oversight, Parmley et al. (1970) utilized MacPherson's technique of analysis to deduce the F/V relationship which is now accepted as that property of the CC occurring in isometric contractions. Conversely, they neglected to put forth the E/F curve which would have been obtained from the isometric F/V data. To date, the true E/F relationship produced by this technique of analysis of isometric contractions does not appear to have been reported in the literature. Therefore, it can only be assumed that the E/F relationship of the SEC is as unique and distinct as the F/V relationship produced during isometric contractions.

iii) The Force-Length Relationship of Both the Parallel Elastic and Contractile Components

a) Parallel Elastic Component

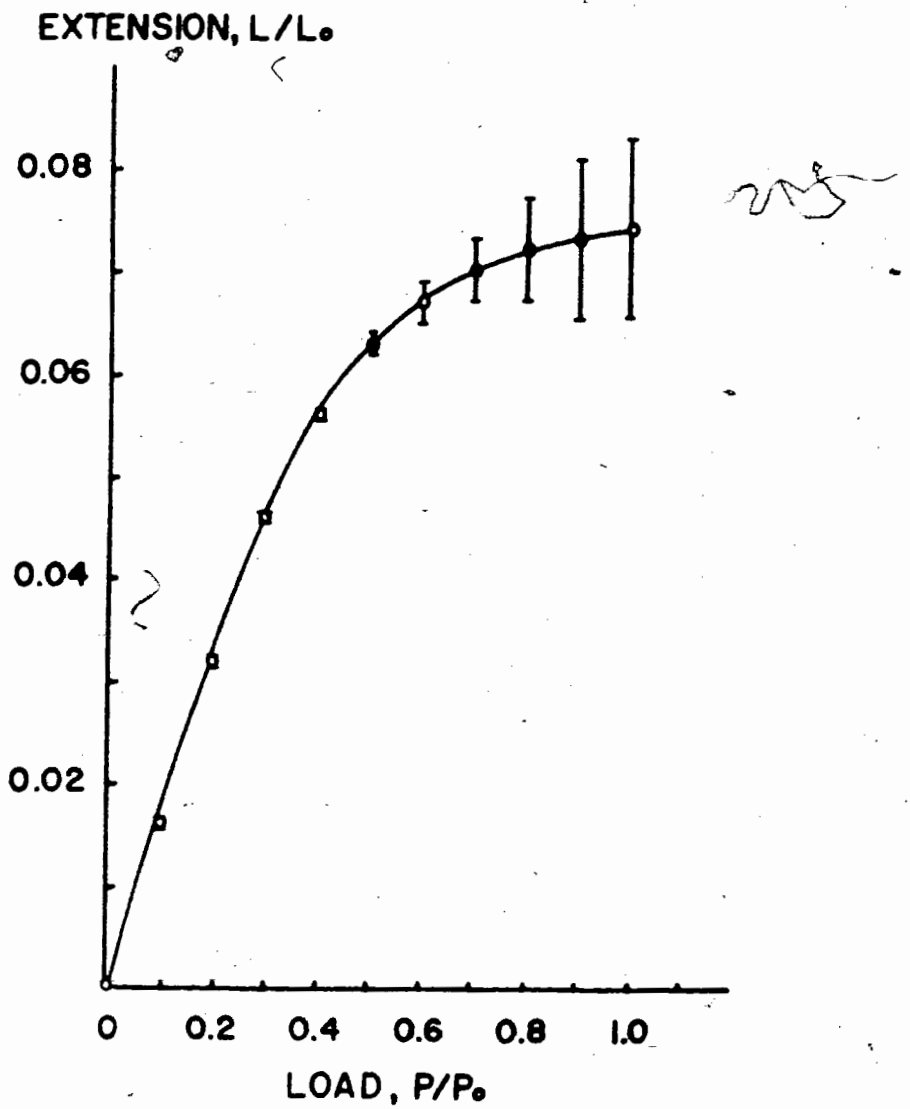
It has been generally accepted that there exists a passive elastic component in parallel (PEC) with the CC and SEC (FIGURE 5). The presence of this component is indicated in a resting muscle when an extension results from the application of a load.

The majority of the structural form of the PEC of Hill's (1950) muscle model has been equated to the tendons of origin and insertion of the examined muscle (Jewell and Wilkie, 1958). Tendon has been found to consist almost entirely of fibres arranged in parallel which correspond with the principal axis of the tendon (Crisp, 1972). These fibres have been shown to be composed mainly of the protein collagen which confers upon the tendon

FIGURE 4:

Extension - force (load) relationship of the series elastic component of the rat gracilis anticus muscle.

(Bahler, 1967; p. 1561)


EXTENSION, L/Lo
0.08
0.06
0.04
0.02
0
0.2
0.4
0.6
0.8
1.0
LOAD, P/Po

flexibility, great tensile strength and relative inextensibility (Elliot, 1965).

The fibre or primary tendon bundle of muscle tendon has been defined as the coherent bundle of collagenous fibrils lying between rows of tendon cells and encircled by their anastamosing processes (Elliot, 1956). Lerch (1950) showed that the primary tendon bundles represented a three dimensional rope-like twisting of collagen fibres. The mechanical properties of this structural arrangement of collagen fibres has been compared to those found for a braided hollow cylinder (ie., Chinese finger lock) (Crisp, 1972). It was shown that the braids or simulated collagenous fibres were disoriented with respect to the long axis of the cylinder at resting length and that under increased force the fibres became longitudinally aligned, thus increasing the resistance to further length deformation. The F/L relationship produced as the result of extension of the braided hollow cylinder was found to be in close agreement with the exponential relationship determined for the extension of the PEC of Hill's (1950) muscle model. Therefore, it has been concluded that the combined mechanical properties of the collagenous structure of the primary tendon bundles determined the mechanical response of the PEC.

Stolov and Weilepp (1966) expanded these observations and suggested that the PEC can be equated to a combination of six anatomical structures: (1) outer connective tissue sheath (epimysium), (2) perimysium and endomysium, (3) sarcolemma, (4) individual fibre content, (5) tendons of origin and insertion and (6) adhesions to neighbouring structures.

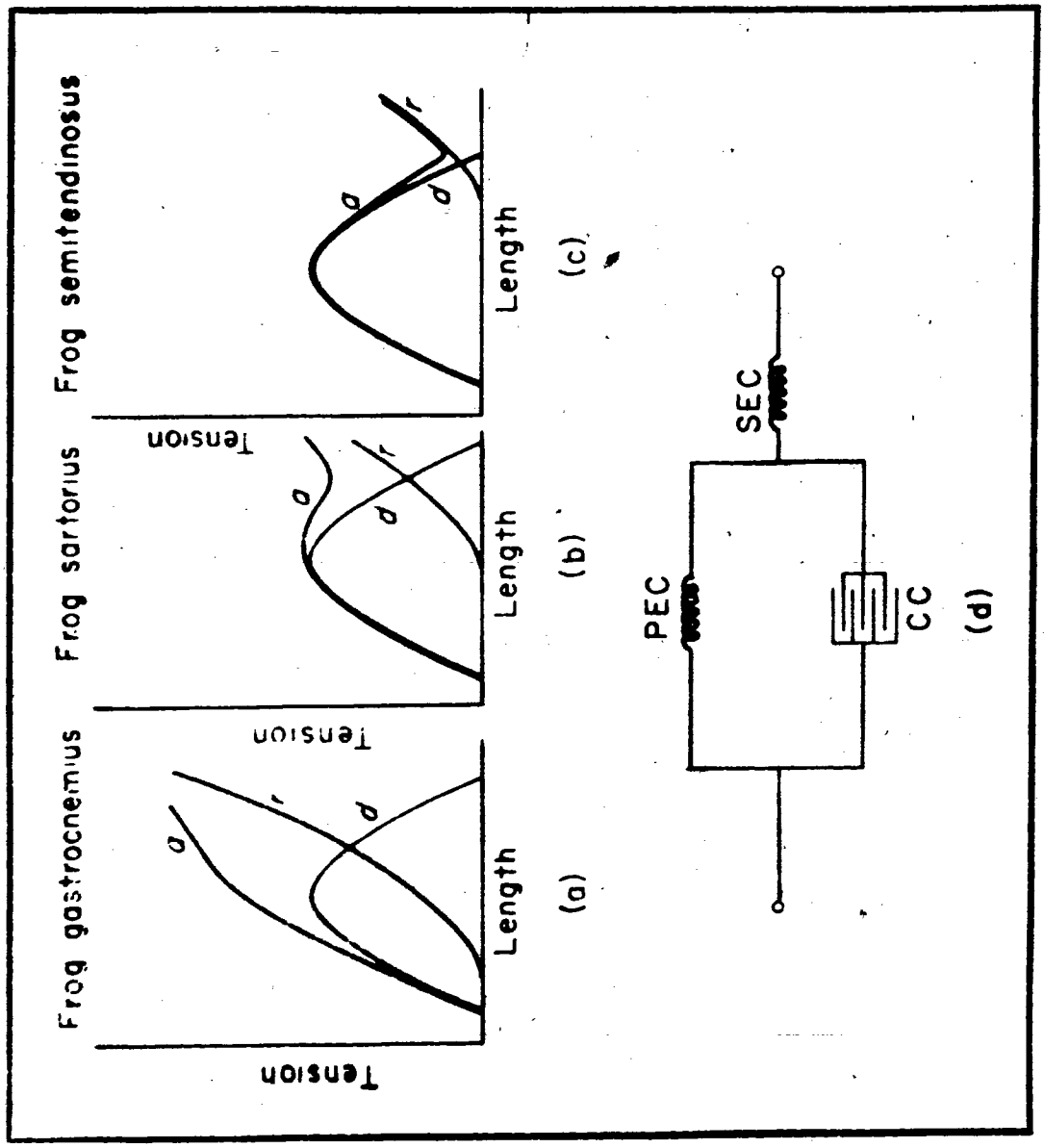
The mechanical properties of the PEC have been presented in the form of an isometric force-length (F/V) relationship for a large number of muscles of different animals (Wilkie, 1963; Stolov and Weilepp, 1966).

FIGURE 5:

(a), (b), (c) The force-length relationship for different muscles. In each case r indicates the F/L curve of the resting muscle, a shows that of the activated muscle and d(=a - r) indicates the force developed by the CC on stimulation.

(d) Equivalent mechanical components in muscle, where:
CC = contractile component
PEC = parallel elastic component and
SEC = series elastic component.

(Wilkie, 1968; p. 30)


Frog gastrocnemius
Tension
Length
o
r
d
(a)
Frog sartorius
Tension
Length
o
r
d
(b)
Frog semitendinosus
Tension
Length
o
r
d
(c)
SEC
PEC
CC
(d)

This relationship has been determined by one of two methods: (1) applying various loads to the muscle and recording the corresponding length (Stolov and Weilepp, 1966; 1970) or, (2) making static measurements of force at various lengths (Abbott and Wilkie, 1953; Wilkie, 1963). The results produced by both techniques are similar in that the PEC does not obey Hooke's law. Increased stretching or loading resulted in the muscle becoming more and more stiff, until a point is reached where irreversible damage occurs. (FIGURE 5), (Wilkie, 1963). This passive relationship has been found to be directly related to the helical structure and mechanical behavior of the collagen molecules which make up the majority of the muscular connective tisses (Crisp, 1972).

b) Contractile Component

When a muscle is stimulated under isometric conditions, the CC develops tension which varies according to the length of the muscle (Gordon et al., 1966; Wilkie, 1953, 1963; Bahler et al., 1968). Since the PEC and CC are mechanically in parallel, the effects of both increased length and stimulation result in a force which is the sum of the combined efforts of both components (FIGURE 5). Therefore the contribution of the CC to the total F/L relationship can be determined by subtracting the efforts of the PEC from the total output of force. A more direct method of measuring the F/L relationship of the CC was devised by Gordon et al. (1966) who observed the effects of length changes on the force generated by a single muscle fibre. Although this technique involved only one fibre, the resulting curve was not unlike that determined for the CC of intact muscle (FIGURE 6a). The most interesting feature of their study was that the F/L relationship could be explained simply by the sliding-filament theory such that the F/L relations of the CC is directly proportional to

the degree of overlap of the filaments (FIGURE 6b).

In a static state, where the muscle was stimulated, the CC developed force which varied according to the length of the muscle or more precisely, the amount of overlap of the myofilaments. Gordon et al. (1966) showed that the active force production of the CC at different lengths was directly proportional to the amount of overlap of the myofilaments (FIGURE 6). They showed that at lengths less than L_o the actin filaments of individual sarcomeres overlapped reducing the number of active sites available for cross-bridge formation. Progressive increases in the sarcomere length towards L_o resulted in increased numbers of active sites on the actin filaments by reducing the amount of overlap of those filaments. Further increases in sarcomere length beyond L_o indicated a progressive reduction in force production as the result of smaller areas of overlap between the actin and myosin myofilaments. Huxley (1957) demonstrated that force production was directly proportional to the number of active cross-bridges. Gordon et al. (1966) succeeded in showing that there was a direct relationship between cross-bridge numbers and force production, but also showed that this relationship was totally controlled by the length of the individual sarcomeres and thus the amount of overlap of the myofilaments. Therefore, with little deviation in the internal structure of sarcomeres, then the shape of the F/L relationship of the CC would be unchanged for skeletal muscles of different animals. Obviously there would be differences in the magnitude of force produced by different muscles but this would be related more to the number of muscle fibres present in the muscle rather than to the structure of the component sarcomeres.

Wilkie (1968) showed the same basic pattern for the F/L relationship of the CC for a number of different frog muscles. He indicated that there

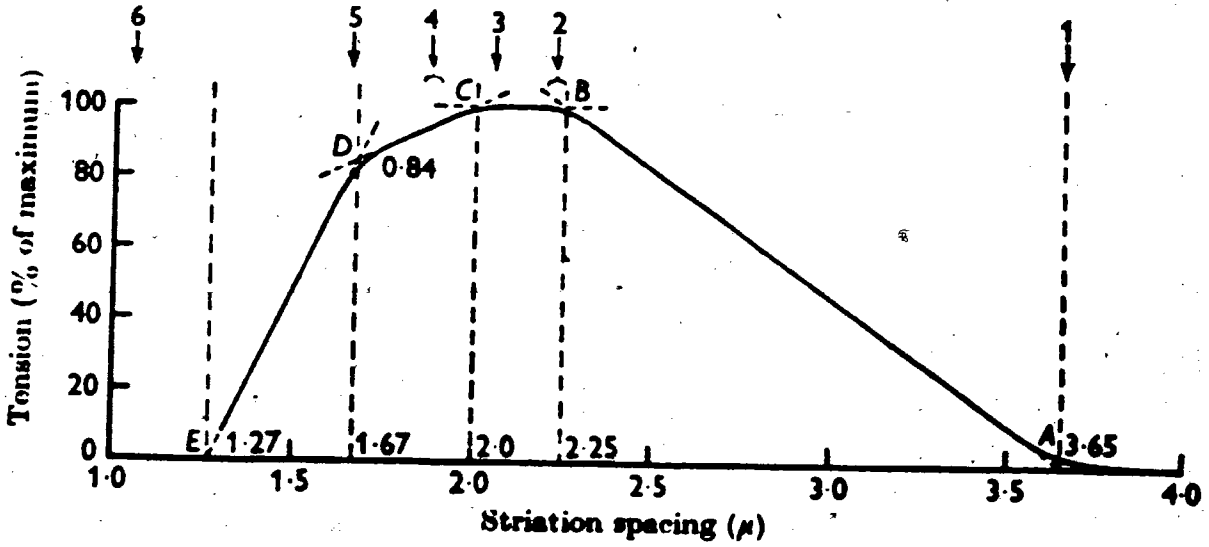
FIGURE 6:

(a) The force-length relationship of the contractile component obtained from a single muscle fibre. The arrows along the top are placed opposite the striation spacings at which the critical stages of overlap of filaments occur; numbers as in FIGURE 6b.

(Gordon, Huxley and Julian, 1966; p. 185)

(b) Critical stages in the increase of overlap between myosin and actin filaments as a sarcomere shortens.

(Gordon, Huxley and Julian, 1966; p. 186)



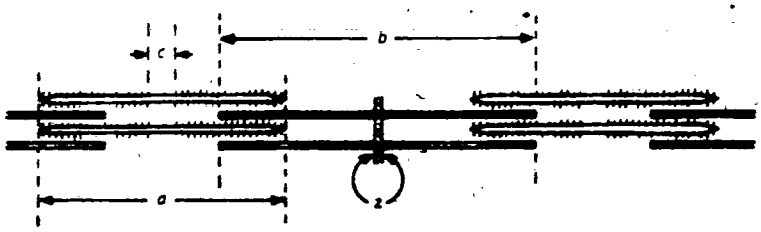
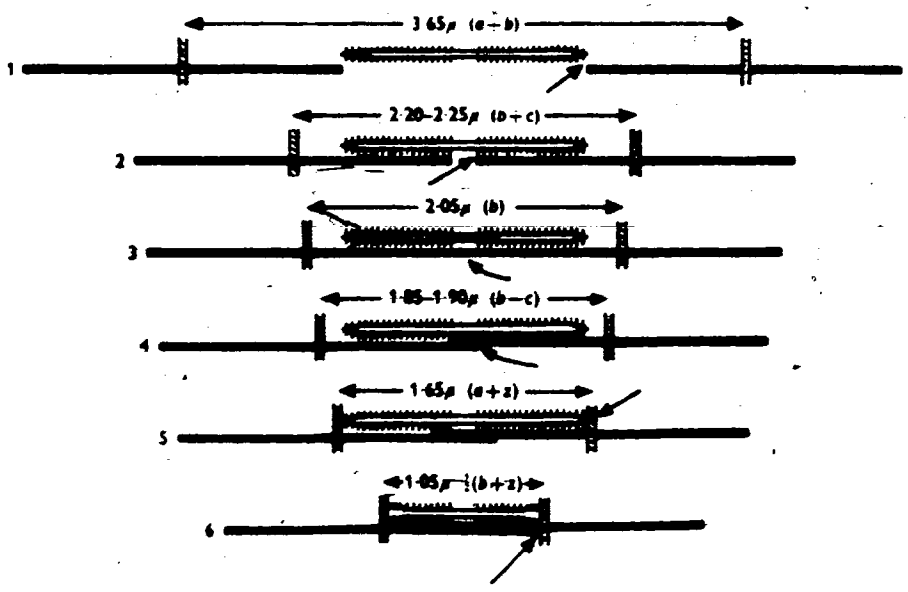


Fig. 18. Schematic diagram of filaments, indicating nomenclature for the relevant dimensions.



were distinct differences in the position of L_0 with respect to the maximal force plateau between the various frog muscles and that these differences resulted in a combined PEC and CC F/L relationship which was unique for each muscle. Virtually no research has been performed with the precise purpose of examining the combined F/L relationship of the PEC and CC in mammalian skeletal muscle. Possibly it was assumed that the F/L relationships of mammalian skeletal muscle would be similar to those found for frog muslce. As Wilkie (1968) has shown, there exists a great difference in the F/L relationships of muscles in one animal which made it highly unlikely that the F/L relationships of muscles of different animals would be the same or even comparatively similar when different modes of locomotion are employed. Although distinct differences were present between mammals and reptiles it has been shown that the process of contraction was identical in a variety of skeletal muscles from a number of different animals. That is, the sliding filament theory was found to apply to most skeletal muscles and the structural format of the filament arrangement did not deviate from skeletal muscle to muscle (Wilkie, 1968). Thus, it would seem that the assumption that the shape of the F/L relationship of the CC would be similar for all skeletal muscles, should prove to be quite correct, although research is necessary to confirm this assumption. It follows then that the differences observed in the relationship between L_0 and the maximal force plateau of different muscles was more likely due to the functional requirements related to locomotion and therefore differences in the amount and distribution of connective tissue in the muscles (Wilkie, 1968).

iv) The Effects of Denervation and Training on the Mechanical Properties of Skeletal Muscle

a) Denervation

The effects of denervation on the structure of skeletal muscle has been well documented. The most evident macroscopic change after denervation is a progressive loss in weight. Following denervation it was found that muscle sustains a loss of weight of up to 30% after one month, increasing to approximately 60% by the end of two months (Sunderland and Ray, 1950; Pelligrino and Franzini, 1963; Elliot, 1965; Hnik, Macloya, Syrovy, Holas and Krishna-Reddy, 1974). Pelligrino and Franzini (1963) determined that the loss of weight was due to two separate processes. In the first a degenerative autolytic process takes place after denervation (up to one month) which results in a loss of striation and the production of a large numer of lysosomes. They suggested that this process represented up to a 50% loss in weight for the individual fibres and it affected each fibre to varying degrees. The effects of the second process were more detectable after one month and resulted in a reduction in the diameter of single myobfibrils. This process was due to the detachment and migration of filaments from the periphery of the fibrils to the interfibrillar spaces. Once these filaments reached the interfibrillar spaces, they were destroyed by the lysosomes which appeared among the fibrils during the first process (Pelligrino and Frazini, 1963; Lewis, 1962). Thus, the volume of the whole fibre was reduced. A more recent study by Miledi and Slater (1969) confirmed that these findings were applicable to the denervated rat diaphragm.

The main process by which the progressive destruction of the contractile material occurred was due to the slow but continuous per-

ipheral detachment of filaments from the fibrils followed by the breakdown of these filaments. Therefore, the fundamental expression of denervation was considered to be the attack and breakdown of the contractile components of the muscle. This would suggest that the ability of a denervated muscle to develop force at any given velocity would be greatly reduced, and the process of reduction would be progressive in correspondance with the progressive loss of contractile material.

Stolov and Weilepp (1966) found that the connective tissue (epimysium, perimysium and endomysium) of the rat gastrocnemius underwent little change with denervation. Also, they found that the muscle lengthened as the period of denervation increased. The latter finding of Stolov and Weilepp (1966) can be explained easily when considering the reduction of volume of individual fibres found by Pelligrino and Franzini (1963). If the connective tissue is considered as a fairly rigid "stocking," being filled with contractile material, then a reduced volume produced by decreased amounts of contractile material would obviously produce an increased length. Although Stolov and Weilepp (1966) found that the connective tissues changes little with denervation, they did find through histological examination that there was an increase in the amount of connective tissue between the muscle fibres. These findings correspond with the results obtained by Elliot (1965). The increase in the amount of connective tissue was demonstrated in the passive F/L relationship developed by Stolov and Weilepp (1966), which indicated that denervated muscle stiffened or became less compliant with increasing days of denervation.

It appears that denervation results in the degeneration or atrophy of one or more of the structural components of muscle. Evidence collected to date indicates that the contractile material suffers the greatest

effects of denervation but virtually no evidence has been presented to demonstrate the effects of these findings on the CC and SEC of Hill's (1950) muscle model.

b) Training

In training, as in denervation, there is well documented histological information on the changes occurring in skeletal muscle. However, there is little or no information on potential changes in the mechanical properties predicted by the components of Hill's (1950) muscle model.

Histological evidence has suggested that a repetitive low-force activity favoured sarcoplasmic protein production and increased muscle mass, while a brief high-force activity increased myofibrillar mass associated with hypertrophy of the muscle fibres, but not necessarily of gross mass (Holmes and Rasch, 1958; Helander, 1961; Gordon, Kasmierz and Fritts, 1967; Lesch, Parmley, Hamosh, Kaufman and Sonnenblick, 1968). Therefore, the effects of exercising on the normal mechanical properties of muscle would be totally dependent upon the exercise program.

When considering a low-force activity like running, an investigator would expect an increase in the muscle mass to be apparant. The previous histological evidence suggested that a low-force activity would not appreciably affect the maximum output of force of a muscle (Barnard, Edgerton and Peter, 1970 Part II). In order to resolve this area of concern it was necessary to take a more precise look at the effects of training on the ultrastructure of muscle fibres before making any statement of expectations concerning the mechanical outputs which might be expected. In fact, Barnard et al. (1970, Part I) found no significant difference between the isometric forces produced by the low-force trained group and

the control. Yet over a period of 60 minutes the trained muscle could maintain a higher level of isometric force than the control muscles. They concluded that the capacity to maintain a higher isometric force exhibited by the trained group might be due to a number of adaptations, including (1) an increase in the capacity of oxidative phosphorylation, (2) an increase in glycogen concentrations, or (3) an increase in the micro-circulation which was indicated by an increase in the capillary-to-fibre ratio. It was interesting to note that these conditons could indeed enhance the stamina of the muscle while having little effect on the force produced during short isometric contraction (Barnard et al., 1970, Part II).

The rat gastrocnemius has been found to be a muscle comprised of three types of fibres: red, white and intermediate (Edgerton and Simpson, 1969). These fibres can be distinguished by using the mitochondrial enzyme succinate dehydrogenase as an indicator of mitochondrial concentration. Further histological examination using the myosin ATPase staining technique would indicate these fibres to be either fast or slow. Barany (1967) found that the myosin ATPase activity was directly related to the actual speed of the muscle, a slow muscle having low activity and a fast muscle higher levels of activity.

Using these techniques, Edgerton and Simpson (1969) determined for rat and guinea pig gastrocnemius that the intermediate fibres were slow, while the red and white fibres were fast. Combined with the findings of Barnard et al. (1970, Part II), of increased numbers of red fibres with no change in the intermediate fibre concentration, one might expect the low-force trained muscle to be faster than the control. As yet there have been no studies performed to demonstrate the true effect of increased

fibre concentration on the mechanical parameters used to describe mammalian muscle.

B. THE EFFECTS OF DENERVATION AND TRAINING ON ANATOMICAL FEATURES OF SKELETAL MUSCLE

i) Muscle Weight (MW) and Body Weight (BW)

It has been inferred that denervation of a group of muscles has little or no effect upon total BW measurements (Stolov and Weilepp, 1966, 1970). Conversely, training has been shown to produce both significant increases and decreases in BW depending upon the training program.

Mayer (1960) suggested that rats will gain BW at an optimal level of enforced exercise but will lose BW if subjected to overactivity. He indicated as did Gordon et al. (1967) that this was the direct result of a food intake in relation to calorie expenditure. Barnard et al. (1970, Part II) found that training reduced significantly ($P < 0.05$ level) the mean BW of guinea pigs. Gordon et al. (1967) had similar results for mean BW measurements of rats trained for varying lengths of the time and different distances of exercise. They found no correlation between distance run and BW and thus questioned the result of Meyer (1960). Gordon et al. (1967) concluded that their results may not have been in disagreement with the findings of Mayer (1960) because it has been shown that the intensity (work per unit time) notduration determined the optimal level of exercise. These observations suggest that BW may be used to indicate the effects of a specific training program but that a better definition of the term optimal exercise is necessary.

A much more direct indication of the effects of denervation and training on muscle has been provided by measurement of MW. Sunderland

and Ray (1950), Miledi and Slater (1969) and Stolov, et al. (1966, 1970, 1973) showed dramatic losses in mean MW which were progressive and represented upward to a 60% loss in mean MW over a two month period of denervation. Sunderland and Ray (1950) all suggested that these losses in mean MW were mainly a consequence of fragmentation of the muscle fibres, with subsequent degeneration of the fragments and disintegration of myomilaments. They found that fragmentation and digestion of myofilaments resulted in reduced volume of the individual fibres which was reflected by increased interfibrillar spaces and decreased mean MW.

Gordon et al. (1967) found for rats trained by low intensity running, isometric work and weight lifting that mean quadricep MW's were reduced but not by a significant amount. Barnard et al. (1970, Part II) determined that there was a significant decrease in weight of the gastrocnemius of guinea pigs trained by low intensity running. Holmes and Rasch (1958) demonstrated an increase in the volume of rat sartorius muscle after running for seven week (six days per week) where the intensity of exercise was increased weekly up to 840 meters per day. They found no increase in the number of myofibrils and concluded that the increased volume was due to increased sarcoplasm. Conversely, Helander (1961) indicated a 15% increase in actomyosin concentrations with no change in sarcoplasm concentrations for guinea pig gastrocnemius trained 1000 meters per day, six days per week. These studies demonstrate that the results obtained for a trained group of animals will vary with the training program. It can be suggested that Holmes and Rasch (1958) used a below optimal or optimal training procedure where increases in exercise intensity were made at equal increments thus allowing the animals to adapt to higher levels of training in a progressive manner. By contrast, Helander (1961) subjected

his experimental animals to beyond optimal levels of activity from the start of the training program. This was indicated when Helander (1961) found his animals becoming exhausted and thus had to introduce two 10 minute rest periods. Although there was little agreement between the distance travelled during training in these studies, the results suggested that the velocity of running and the method by which this velocity was introduced were the deciding factors in muscle adaptation to training. This observation was originally presented by Petov and Siebert (1925) (cited by Gordon et al., 1967).

Referring to the conclusions of Gordon et al. (1967), some observations can be presented. Barnard et al. (1970, Part II) showed reduced MW for trained guinea pigs, but found no change in maximum isometric force. However, the trained muscles were able to maintain a higher level of isometric tension over a period of 60 minutes. This data indicates an increased level of endurance with no increase in strength, thereby suggesting increased sarcoplasmic protein concentrations for the trained muscles. Therefore, the measured decrease in mean MW was not related to changes in the mechanical properties of guinea pig muscle due to training. Obviously the suggested relationship between increased MW and sarcoplasmic protein concentration presented by Holmes and Rasch (1958) does not stand true when indicated by the changes in mechanical properties. Thus, it must be concluded that other circumstances were involved in producing the inconsistant results of Barnard et al. (1970), Part II).

ii) Muscle Length (ML)

It has been demonstrated that mean ML does not change significantly after an extended period of training (Goldberg, 1967). In contrast,

prolonged denervation has been shown to increase the mean ML of muscles (Stolov and Weilepp, 1966, 1970).

Stolov and Weilepp (1966, 1970) demonstrated increases in mean ML over a period of four months of denervation. They showed that these increases were significant up to and including three months after denervation and that there were no significant changes in mean ML between the third and fourth month. There was found to be a slight increase in mean ML during the period of denervation and increased ML was exponential. They concluded that dramatic changes in mean ML occur during the early periods of denervation and are reduced in magnitude as the period of denervation increased.

Stolov et al. (1970) summarized that elongation of the gastrocnemius due to denervation may have been the result of one or a combination of all of the following: muscle atrophy, the loss of plantar flexion or a relative decrease in collagen. Muscle atrophy or loss in MW may have a unique effect on gastrocnemius which would result in much larger increases in ML when compared to other muscles suffering the effects of denervation. The rat gastrocnemius is a pennate muscle where individual muscle fibres originate and insert along a tendinous sheath which is continuous with the tendons of origin and insertion. Thus the plane of contraction of individual muscle fibres would not be continuous with the plane drawn between the tendons of origin and insertion. Stolov et al. (1970) concluded that fibre atrophy would result in decreased volume of the muscle and thus increase the distance between the tendons of origin and insertion. Therefore, muscle atrophy of the gastrocnemius would have resulted in a passive and progressive increase in muscle length which would correspond with decreases in muscle volume.

The loss of plantar flexion due to denervation of the gastrocnemius would result in shortening of the antagonist muscles and permanent dorsi flexion. The dorsi and plantar flexor muscles work as a unit, actively controlling the range of movement around the ankle joints. Shortening of one of these groups of muscles would be limited by the structure of the joint and more directly by the antagonist group of muscles. Thus, elimination of the contractile capacities of one of these groups would result in virtually no control or length changes of the other muscle group.

It seems highly unlikely that elongation of a denervated muscle would be partially the result of reduced collagen content. Stolov et al. (1970) showed a decrease in total hydroxyproline, the characteristic amino acid of collagen. They concluded that the reduced total hydroxyproline was not necessarily indicative of a loss in muscle collagen but might indicate a slower rate of accumulation in denervated muscle. Sunderland and Ray (1950) showed a relative increase in connective tissue between individual muscle fibres of denervated muscle when compared to the content of control muscle. The combined results of these studies suggested that although connective tissue concentrations may increase a major component of connective tissue, collagen might very well demonstrate a slower accumulation rate during denervation around the individual muscle fibres.

iii) Types of Muscle Fibres

All striated muscle fibres are similar in gross structure and function, but there are morphological and cytochemical differences which suggest inequalities between fibres. Some of these differences are observed in: 1) colour, 2) fibre diameter, 3) mitochondrial content and distribution, 4) size and shape of myofibrils, 5) ultrastructure of

sarcomere, 6) phosphorylase activity, 7) glycogen content, and 8) triglyceride content (Gould, 1973). Three distinct muscle fibre types have been described using these criteria: red, white and intermediate (Henneman and Olson, 1965; Edgerton et al., 1969; Gould, 1973). Red fibres have been found to be small in diameter and display a large number of mitochondria. White fibres, on the other hand, have been characterized by a larger diameter and insignificant amounts of mitochondria in relation to the red fibre content (Gould, 1973; Sisson, 1974). Intermediate fibres have been accepted as those fibres demonstrating mitochondrial and dimensional properties which lie between the red and white fibres.

Henneman et al. (1965) indicated that fibre composition of cat gastrocnemius varied within the muscle such that the percentage composition of red, white and intermediate muscle fibres ranged from 9.4 to 31.2, 46.4 to 58.5 and 21.3 to 36.4 respectively. For the medial gastrocnemius they determined that red fibres represented 27%, white 50.9% and intermediate 21.3%. Barnard et al. (1971, Part I) found for the medial gastrocnemius of guinea pigs that the percent totals were: 50.2% red, 38.6% white and 11.7% intermediate. It is obvious from these results that large differences exist between the same mammalian muscle of different animals. These differences have been suggested to be the result of different modes of locomotion and thus different mechanical requirements of the muscles (Close, 1972).

As far back as 1935, it was suggested by Tower (1935) that denervated muscle tissue progressively lost its specific characteristics becoming transformed into fibrous tissue. She described the transformation of muscle fibres to fibrous tissue as fibrotic dedifferentiation. Altschul (1942) observed similar changes in denervated cat and rabbit muscle but

suggested that the replacement of muscular tissue by connective or fibrous tissue was accompanied by increased concentrations of fatty tissue. These authors concluded that degeneration or atrophy of the individual muscle fibres resulted in a progressive replacement of muscle fibres with connective tissue and small amounts of adipose tissue.

More recent research performed by Sunderland and Ray (1950) showed increased connective tissue concentrations during a period of denervation, but at no stage were atrophying muscle fibres replaced by fibrous tissue. They indicated that proliferation of connective tissue initially appeared in the perimysium during the first month of denervation and that after two months significant increases in connective tissue concentrations were observed in the epimysium and endomysium. After a period of three months it was shown that the individual muscle fibres were no longer packed tightly together but were separated by an extremely inflated endomysial layer of connective tissue. These authors concluded that denervation was characterized by a sharp decline in the volume of individual muscle fibres and an increase in the amount of connective tissue around these fibres.

Adams, Denny-Brown and Pearson (1965) stated that the large histochemical and dimensional differences observed between red and white muscle fibres were virtually lost during prolonged denervation. They indicated that degeneration of these muscle fibres progressed, at different rates, to a level where both fibre types were approximately the same size and demonstrated the same histochemical properties. It was concluded that prolonged denervation resulted in more dramatic changes in fibre size of the white fibres and histochemically indicated activity of the red fibres.

Edgerton and Simpson (1969) demonstrated that rat gastrocnemius,

like guinea pig gastrocnemius, comprised of three types of muscle fibres: red, white and intermediate. Bárány (1967) found that the speed of contraction of a muscle was directly proportional to the level of myosin ATPase activity, where a slow muscle was represented by low myosin ATPase activity and higher levels of activity were indicative of fast muscle. Employing the observations of Bárány (1967), Edgerton and Simpson (1969) determined for rat and guinea pig gastrocnemius that red and white muscle fibres were fast contracting while intermediate fibres were slow. Barnard et al. (1970, Parts I and II) found that trained guinea pig gastrocnemius exhibited greater motochondrial protein concentrations, a greater capacity for oxidative phosphorylation and a significant increase in the percentage of red fibres, when compared to the sedentary or control muscle. Combining the findings of Edgerton and Simpson (1969) and Bárány (1967) with the results of Barnard et al. (1970, Parts I and II) it is suggested that the method of training used by Barnard et al. (1970, Parts I and II) should have significantly increased the speed of contraction of the muscle as indicated by the increased numbers of red muscle fibres and mitochondrial protein concentrations. Barnard et al. (1970, Parts I and II) indicated that there was only a small difference in total rise time of force production.

C. SUMMARY OF RELATED LITERATURE

There is sufficient evidence now to show that mammalian skeletal muscle, like frog skeletal muscle, contains three interacting components: the contractile component (CC), the series elastic component (SEC) and the parallel elastic component (PEC). The mechanical parameters of each of these components have been widely demonstrated to be nonlinear.

Investigations into the mechanical responses of muscle during activation have shown that there were distinct differences in the F/V relationship of the CC obtained from dynamic and isometric contractions. Although these differences have been documented to be quite dramatic, researchers have neglected to examine in detail the mechanical properties of the SEC during the same isometric conditions. It has been inferred in the literature that the characteristic E/F relationship of the SEC was the same for both types of contractions. One of the purposes of this thesis will be to examine the mechanical properties of the CC and SEC during isometric contractions by applying a technique developed by MacPherson (1953).

Houk (1963) presented a model for striated muscle which assumed linear approximations of the mechanical parameters of activated muscle. The best linear fit to the nonlinear "classic" isotonic F/V relationship was used in conjunction with the isometric myogram to deduce the linearized compliance of the SEC. However, it is known that different F/V relationships are obtained from isotonic and isometric contractions. It is hoped that the present study will reveal the degree to which changes in nonlinear properties are reflected by changes in the linearized properties obtained during isometric contraction. It is hypothesized that these changes will result from denervated and training of the gastrocnemius muscle of the rat.

The effects of denervation and training on muscle structure and anatomical measures have been examined by histochemical, histological and biochemical techniques. Very little work has been performed with the expressed purpose of evaluating the effects of these conditions on the mechanical properties of the various components of Hill's (1950) model.

The F/L relationships of the CC and PEC will also be examined.

Although the F/L relationship of the PEC has been well documented for both mammalian and reptilian muscles, the same relationship has been somewhat overlooked for the CC of mammalian muscle.

CHAPTER III

MATERIALS, METHODS AND PROCEDURES

A. EXPERIMENTAL MATERIAL

The experiments were performed on the gastrocnemius muscle of the right leg of thirty-two white male Sprague Dawley rats approximately nine months old. The range of body weights was 500 - 800 grams and the rats were fed a normal balanced diet. They were separated into three groups: the sedentary or control (N = 10), trained (N = 10) and denervated (N = 12).

Each group was then divided into two unequal subunits for use in the F/V and F/L studies; see TABLE 1. The larger subunits of each of the three groups were used to quantify the effects of denervation and training on the mechanical properties of the linear and non-linear models. The denervated group used in this study was divided further into two equal groups which were tested one month apart to determine the effects of prolonged denervation on the mechanical properties of the two models.

The remaining subunits were used to determine the effects of the various experimental treatments on the static properties of the PEC and CC at different muscle lengths. Furthermore, both of these denervated and sedentary subunits were divided equally and then tested one and two months apart respectively. The purpose of this division was to determine the effects of prolonged denervation and aging on the static properties of the muscular components.

In addition one sedentary and one denervated rat provided muscle tissue which was used in the histological and histochemical part of this thesis.

TABLE 1:

THE VARIOUS TYPES OF TREATMENTS APPLIED TO THE GROUPS OF RATS AND THE EXPERIMENTS TO WHICH THEY WERE SUBJECTED.

GROUPS	NUMBERS IN SUBUNITS	AIMS	TREATMENT
SEDENTARY (10)	6	linear and non-linear analysis	Kept in cages without specific exercise
	2 2	F/L relationships (PEC & CC), two months between groups	
DENERVATION (12)	4	linear and non-linear analysis for one and two months after denervation	Kept in cages, lesions of the tibial nerve of appropriate level to render both soleus and gastrocnemius muscle inoperative.
	4		
	2 2	F/L relationships (PEC & CC), one and two months after denervation	
EXERCISED (10)	8	linear and non-linear analysis	Normally kept in cages but exercised on an inclined treadmill three times a week for 30 minutes at one half to one mile per hour (8 months).
	2	F/L relationship (PEC & CC)	

B. METHODS

i) Apparatus

a) Muscle Support Systems

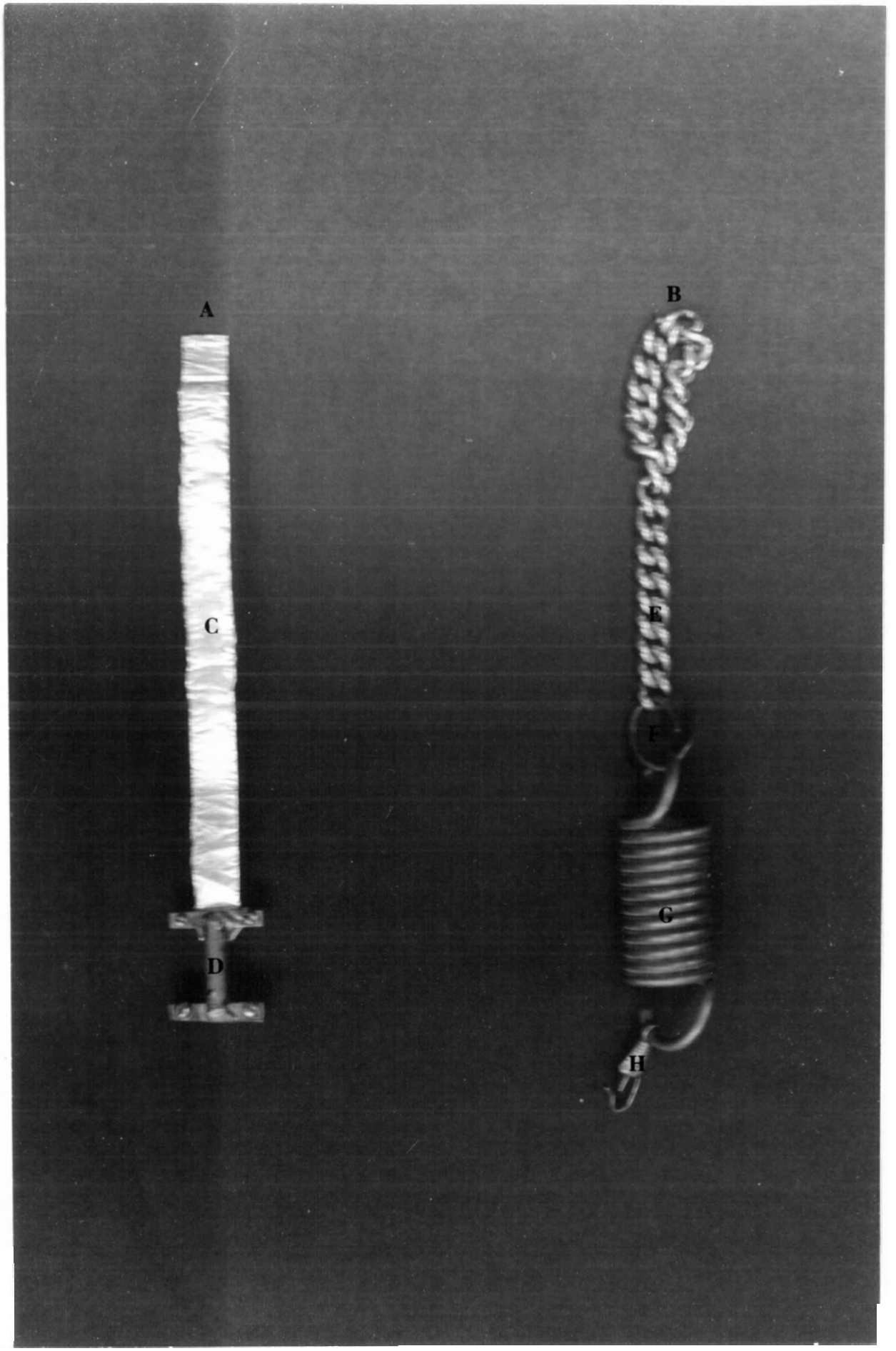
The most important apparatus involved in these experiments were the muscle support systems. The various securing mechanisms used were designed to incorporate the actual bones attached to the origin and inserting tendons of the rat gastrocnemius.

The origins of the two-headed gastrocnemius are the two femoral condyles. To eliminate damage to the tendons of origin, the distal part of the femur, one centimeter (cm.) in length, was removed with each muscle. A hole, 0.16 cm. in diameter, was drilled through the patellar surface along a line corresponding with the long axis of the shaft of the femur. This hole alowed accomodation of a threaded stud which protruded from the force transducer. This section of femur was then secured, with the patellar surface snug against the force transducer face, by an accompanying nut. This method of femoral attachment did not vary for any of the experiments performed.

Attachment of the insertion bone (calcaneus) presented different problems which were due to its size and the type or method of experimentation. The tendo-calcaneus, which is the insertion tendon of both the gastrocnemius and the soleus muscle, inserts into the posterior portion of the calcaneus (Wells, 1966). In the rat the calcaneus is a relatively small bone comparable in size to the inside diameter of the femoral shaft. Due to the small size, the calcaneus did not lend itself to procedures involving the drilling of holes or pin retainers. The major difficulties found with these techniques were weakening and shattering of the bone, and it was decided that a system was needed which incorporated

PLATE 1:

Support systems for the force-length (A) and the force-velocity (B) studies. The support system for the strap (C) is shown along with a double-headed brass clamping mechanism (D) which secured one end of the aluminum strap and the calcaneus. The support system for the force-velocity study was made up of a jeweller's chain (E), a connecting metal loop (F), a spring (G) with a compliance of 0.0001 cm./gm. wt. and a jeweller's watch clasp (H) which secured the calcaneus.


A
B
C
D
E
F
G
H

the intact bone.

A double-headed brass clamping arrangement was designed to accomodate the calcaneus in the F/L experiments. Each head had a base plate fixed permanently to a brass tube 2 cm. in length. These base plates were fixed perpendicular to the long axis of the tube and muscle. A notch was cut into both ends of the brass tube so that the base plates fitted snugly within them before being soldered. Two identical pieces of brass plate were matched and each attached to the fixed plates by a pair of screws measuring 0.32 x 1.0 cm. (PLATE 1). One pair of plates secured the calcaneus while the other clamped on to one end of a flexible aluminum strap 6 cm. in length. The other end of the strap was then clamped in a similar system to the solid metal displacement drum. The displacement drum, 5 cm. in circumference, was directly connected to the displacement transducer by a drive coupling (PLATE 2). Manual rotation of the drum resulted in a directly proportional change in muscle length because the compliance of the strap support system was much less than that of the muscle.

The compliance of the strap support system was tested by fixing the free end of the aluminum strap to the displacement drum and hanging different sized weights on the free brass clamp. Length changes of the system were measured by a telescopic micrometer for weights up to and including 3 kilograms (Kg.). As there were no length changes recorded for all the weights tested, the compliance of the support system was found to be less than 1/100 of a cm. within the range tested.

The F/V technique of analysis developed by MacPherson (1953) required at least one pair of isometric contractions, one with the other without an added compliance. Houk's (1963) system of analysis nec-

essary to produce a large number of both types of isometric contractions where at least one of each reached the same final magnitude of force. To accomodate these changes, a solid steel platform was used which had a fixed vertical shaft, 30 cm. long, with a vertically adjustable horizontal arm attached. The calcaneus was secured by wedging it into a jeweller's watch clasp while a jeweller's chain, 8 cm. long (links of wire 2.26 mm. in diameter), was secured to itself around the adjustable horizontal support arm (PLATE 3). The looped end of the watch clasp was then attached to the loose end of the chain by an overlapping loop of wire 2.20 mm. in diameter. The compliance of this system was determined to be zero by using the telescopic micrometer and a variety of weights up to 3 Kg.

Rotation of the connecting metal loop from the experimental position resulted in the freeing of the watch clasp. At this point the spring was added by placing one hooked end through the watch clasp while the other end was hooked through the wire loop (PLATE 3). Adjustments for the added length due to the spring were made by hand-cranking the horizontal arm upward. With the spring in place, the compliance of the system was equal to that of the added spring because it was earlier determined that there was zero compliance in the remaining support system.

b) Added Compliance

The single most important piece of apparatus for the F/V experiments was the added series compliance or spring. Parmley and Chuck (1973) quantified the mechanical effects of added compliance on isometric contraction. Their results indicated that there was a reduced level of force production which was directly related to the length changes afforded by the compliance of the spring placed in series. However, MacPherson's (1953) system of analysis required that two contractions, one with and

PLATE 2:

The displacement transducer (I), displacement drum (J), stimulating electrodes (K) and the force-length support system (A) in position.

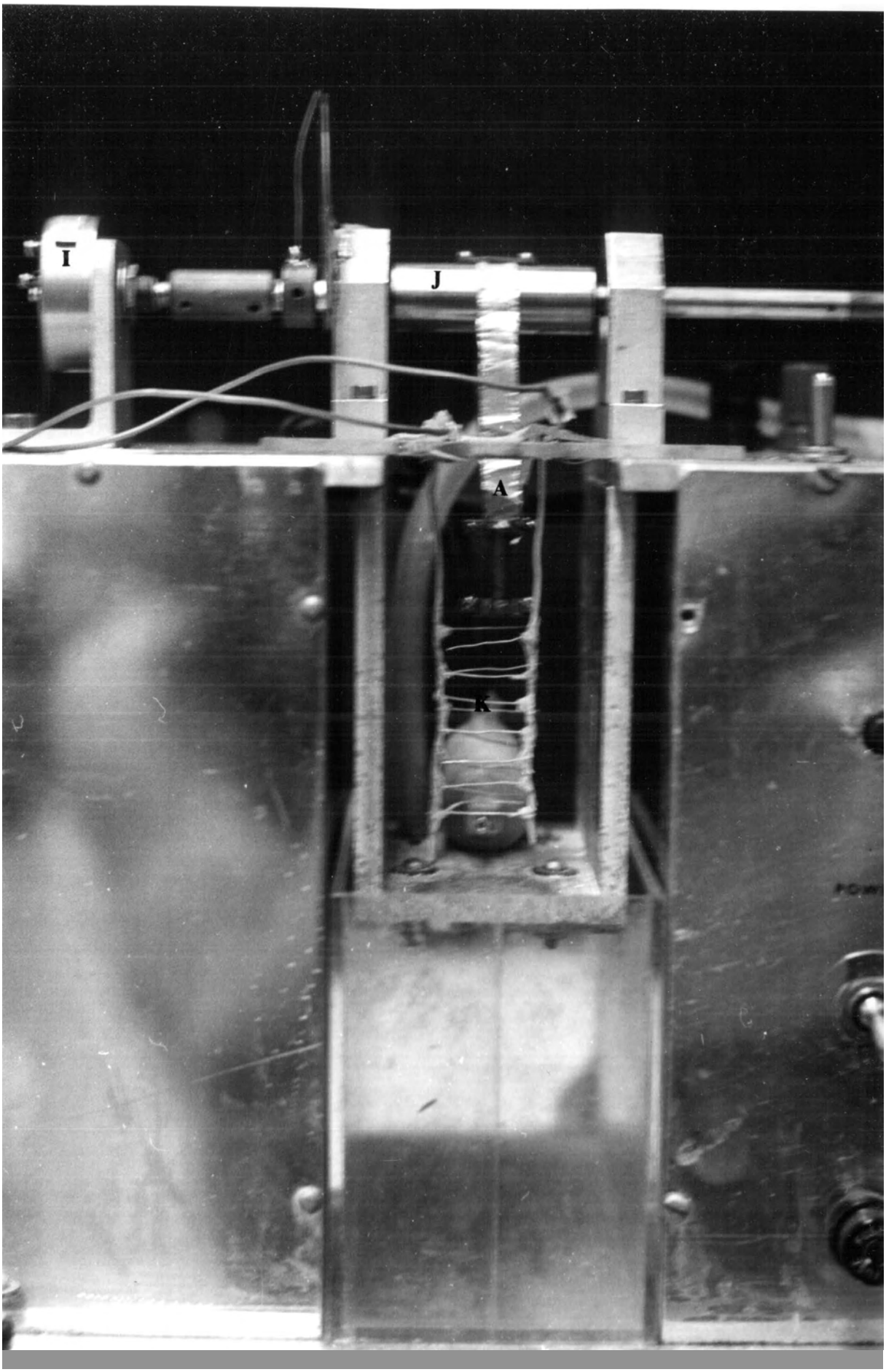
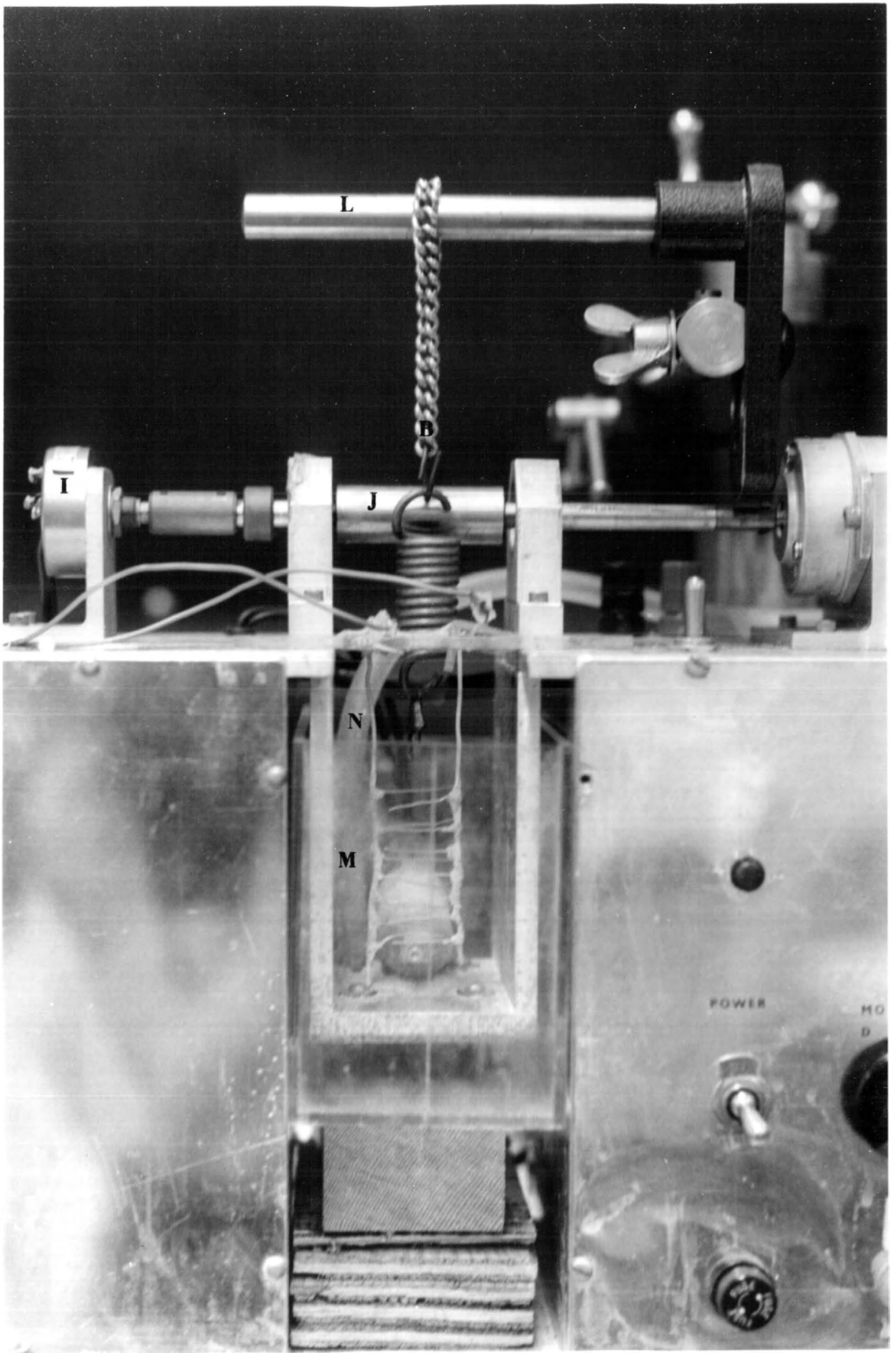

I
J
A
K

PLATE 3:

The support apparatus used in the force-velocity study. The adjustable support arm (L) secured one end of the support system (B) while the other end retained the calcaneus. The Ringer's solution bath (M) is shown in the experimental position with the oxygenation tube (N) in place. The displacement transducer (I) and drum (J) are shown but play no part in experimentation for this study.


L
B
I
J
N
M
POWER

the other without an added compliance, must have the same magnitude of force. Therefore it was necessary to incorporate an added series spring which should have properties of compliance not only similar to those of the SEC but small enough to negate large changes in muscle length.

MacPherson (1953) introduced an added series spring with a compliance of 0.002 cm./gm. wt. for the study of frog sartorius muscle. Due to conclusions found in the literature concerning the SEC compliance in different animals, the added compliance used by MacPherson (1953) cannot be used in studies involving rat skeletal muscle. Therefore, experiments were conducted to determine the appropriate series compliance for rat gastrocneumius which would result in the fulfillment of MacPherson's criterion. A group of ten springs were examined and their E/F characteristics recorded. A telescopic micrometer, accurate to 1/100 of a centimeter, was used to measure the extension of each spring at various loads, increasing from zero to three Kilograms weight. If the spring tested did not obey Hooke's Law throughout the experimental range, it was discarded. Of the ten original springs, only seven remained whose mechanical properties were linear. Their individual compliances were: one at 0.0006, two at 0.0004, one at 0.0003 and three at 0.0001 cm./gm. wt.

Experiments were then conducted on the remaining springs to determine the level of added compliance which best approximated the compliance of the SEC. That is, these springs were examined to determine the level of added compliance which produced a definite difference in the isometric-rise-time while still producing a magnitude of isometric force comparable to the contractions without an added compliance. It was found, and later tested several times, that an added compliance of 0.0001 cm./gm. wt. produced the best comparable results. Furthermore, only one of the

three springs with this compliance was selected to perform these studies. The two remaining springs were eliminated because of either their large diameter or extreme length.

c) Transducers of Force and Length

The force transducer[1] was a horizontal, rigid steel "I" beam incorporating two resistance foil strain gauges enclosed in a watertight cylindrical nylon mounting. It was fixed securely to the bottom plate of a 5 cm. wide, U-shaped submersion platform (PLATE 4). Embedded in the end of the transducer beam and protruding from it was a threaded rod with the dimensions of 0.16 x 3.0 cm. The femur of the muscle tested was placed upon the rod and secured by a nut. Force exerted upon this unit created voltage which was directly related to the deflection force. Initial calibration of the unit determined a linear response between voltage output and deflecting force with a mean error of 0.9%. The linear response was found to be identical in the reverse (180°) situation, but a cross-torque of 4.5% was indicated at a perpendicular deflection from the experimental position. The cross-torque was discounted because the force transducer was securely fixed in an upright position where no rotation was possible (PLATE 4).

The displacement transducer[2] used for the F/L study was a commercially made unit which was attached by a drive coupling to the displacement drum which was 5 cm. in circumference (PLATES 2, and 4). Calibration figures were acquired through repeated 0.7 mm. movements of the drum which were measured on a fixed protractor by an indicator arm

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[1] Designed and constructed by A.E. Chapman, Department of Kinesiology, Simon Fraser University.

[2] Type 151-5853B, 16 K 7143 Transducer, IRC, St. Petersburgh Division, TRW Inc.

PLATE 4:

The force transducer (O), oxygenating tube (N) and one litre Ringer's solution bath (M) before commencement of experimentation. The force transducer beam, which incorporates foil strain gauges, is enclosed in a cylindrical nylon mounting. The lower end of the femur is drilled along the shaft of the bone, placed on the threaded rod which protrudes from the transducer beam, and secured by a nut (P).

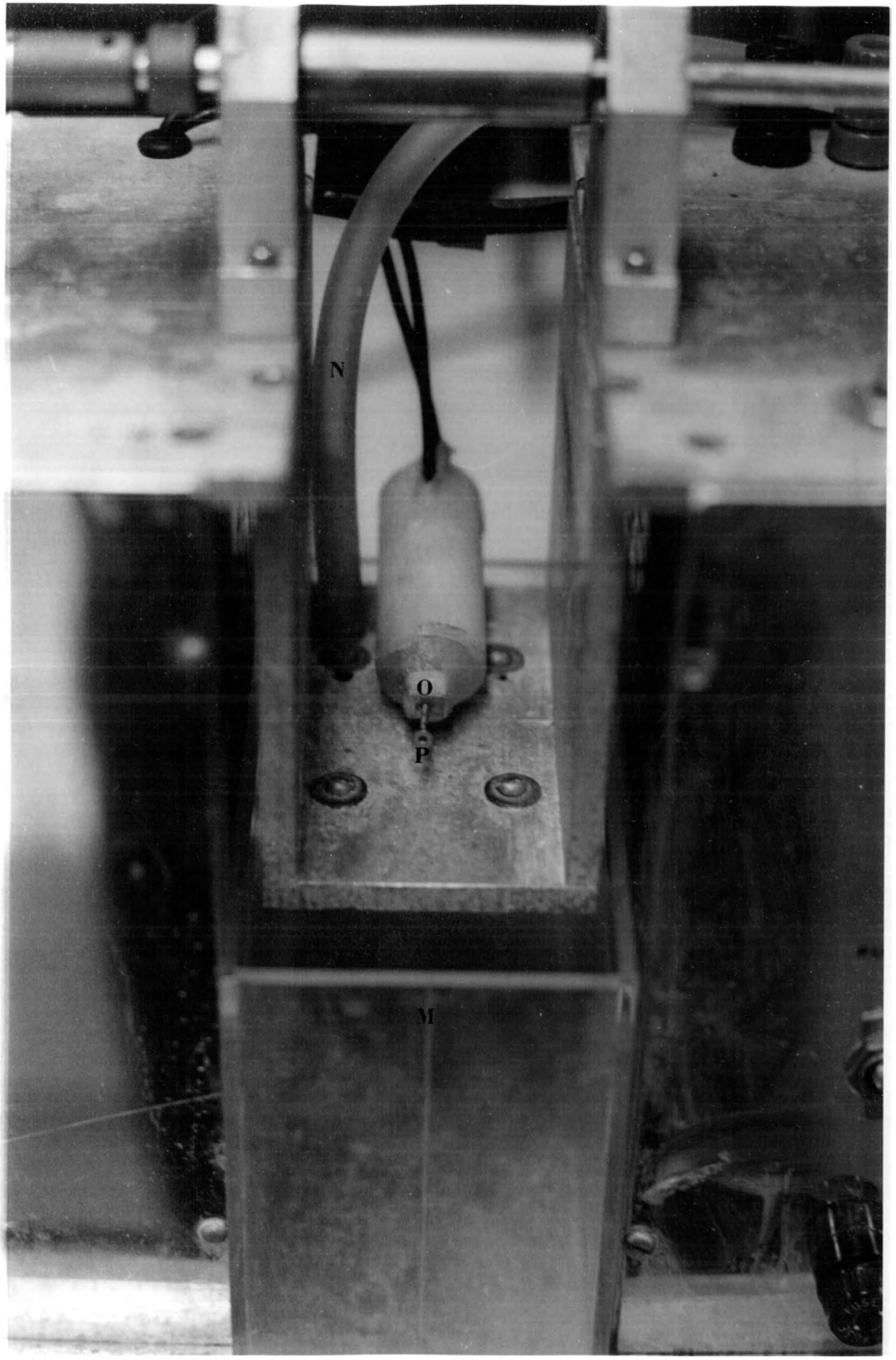

N
O
P
M

PLATE 5:

The apparatus used for recording and display. Explanation of reference letters are for PLATES 1 to 4. In addition, the following reference letters apply:

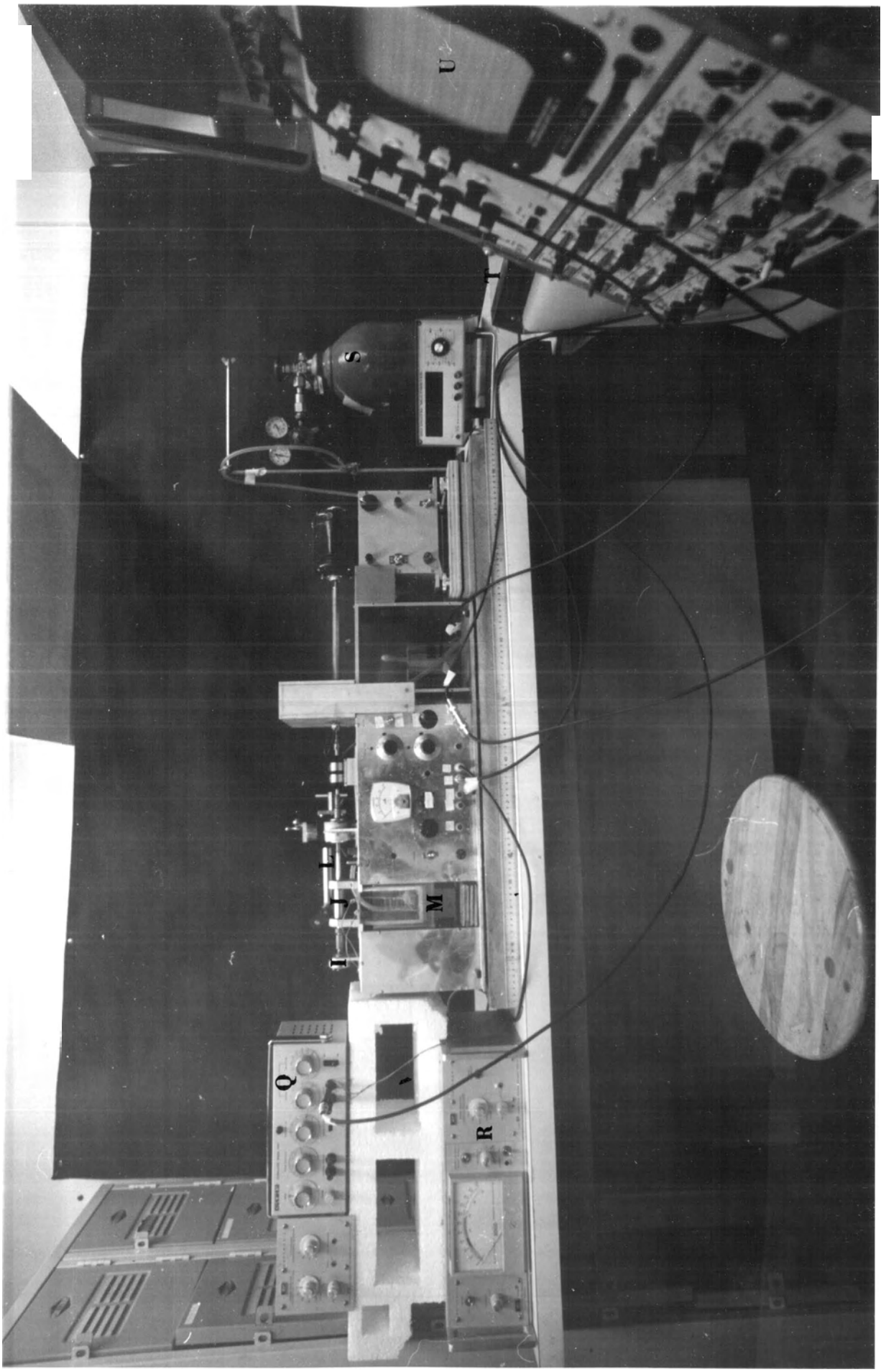
(Q) C.F. Palmer Stimulator. Square wave output 0 to 25 volts, pulse width 0.1 to 5 msec., frequency 0 to 120 Hz.

(R) Daytronic Strain Gauge Amplifier containing a model 300D meter with a type 91 strain gauge transducer input module and a type-P galvanometer driving output module.

(S) Compressed Gas Cylinder containing 95% O_2 and 5% CO_2 with flow control gauges.

(T) Bell and Howell Ultraviolet Recording Oscillograph for permanent recording of outputs from stimulator and transducers of force and displacement.

(U) Eight-Channel Display and Galvanometer Driving Amplification Unit (Teca Unit).


U
T
S
L
M
Q
R

attached to the drive coupling. This procedure was repeated several times in both directions resulting in a linear response (error ± 0.03%).

d) Amplification and Display

A Daytronic strain gauge amplifier with plug-in modules was used to amplify the voltage changes obtained from the force transducer (PLATE 5). This unit contained a model 300D indicator or meter with a type 91 strain gauge transducer input module and a type-P galvanometer driving output module. This strain gauge transducer input module had a range selector which reduced the transducer input and thus the output to the galvanometer by varying percentages for full scale meter deflection. The experiments conducted involved the use of amplification levels of 10% for the denervated muscles and 50% for the sedentary and trained.

The output from the strain gauge amplifier, the displacement transducer and the stimulator[3] were fed through an eight channel display and galvanometer driving amplification unit[4] to a Bell and Howell ultraviolet recording oscillograph[5] (PLATE 5, FIGURE 7). Only the output from the strain gauge amplifier was passed through a 0 to 15 Hz. filter (-3 db point) before entering the Teca Unit. The Teca Unit was used strictly for driving and adjustment of galvanometer deflections in the ultraviolet recorder. Prior to every experiment the scales of deflection of the galvanometers were checked to insure linearity of response for the force and displacement inputs (APPENDICES 1, 2 and 3).

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[3] Model 8043, Stimulator, C.F. Palmer, London, England.

[4] Model TE8, Teca Corporation, White Plains, N.Y., U.S.A.

[5] Model 5-127, Bell and Howell Ltd., Consolidated Electrodynamic Division, Basingstoke, England.

The ultraviolet recorder produced 0.1 second time lines which were perpendicular to the long axis of the recording paper. The frequency of these time lines was calibrated to determine accuracy by recording an external input of known frequency. It was determined that the time lines occurred at 0.097 second intervals which represented a 3% error from the stated time interval. This error was ignored because it was both consistent and of a small magnitude.

e) The Stimulator

Square wave stimulation was applied to the muscle through a pair of multi-element platinum electrodes placed in contact with and on opposite sides of the muscle (PLATE 2 and 3). Thus the electric field was perpendicular to the long axis of the muscle while the polarity of the electrodes was changed manually after each contraction to minimize the effects of polarization.

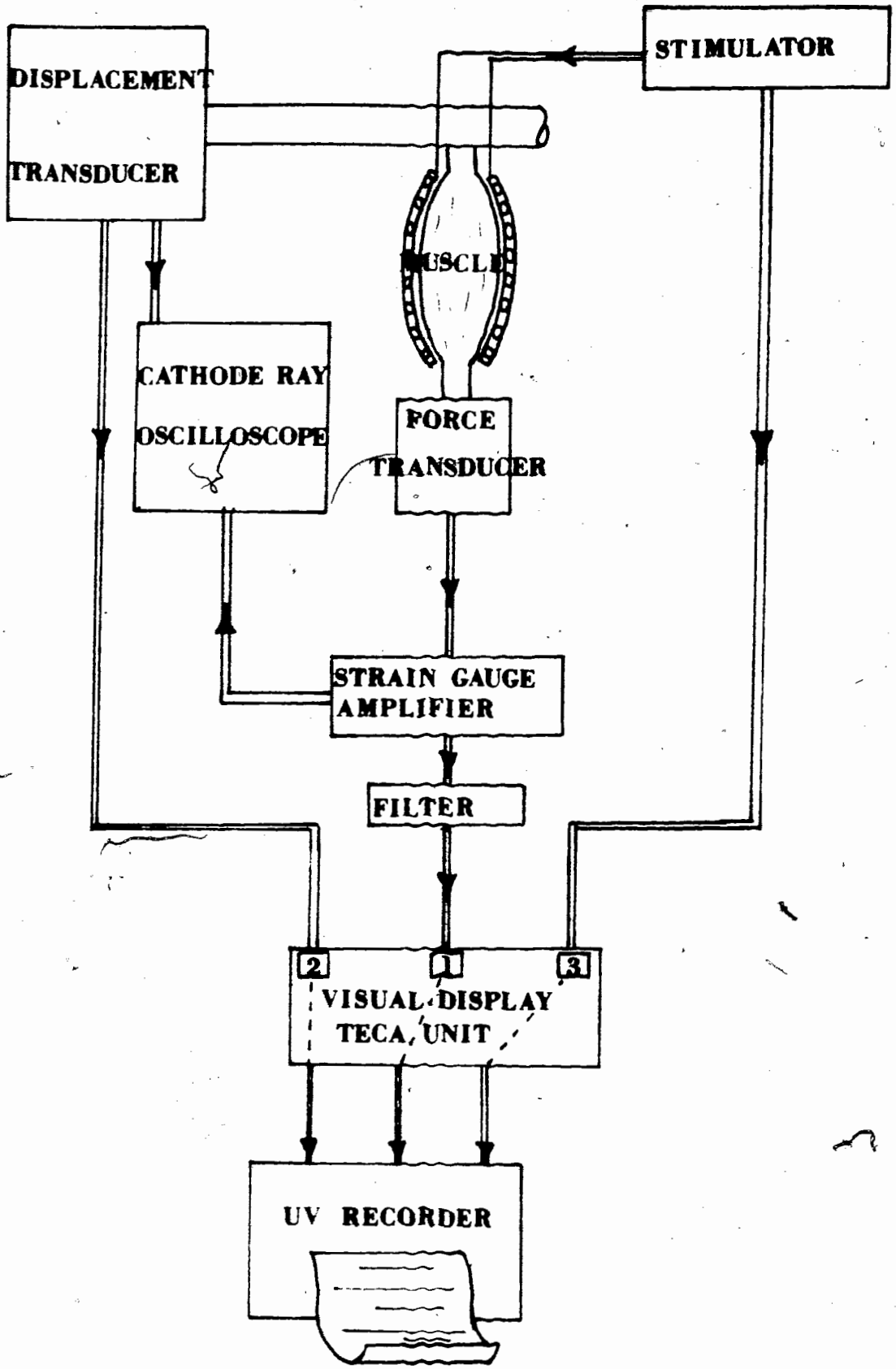
A series of five preliminary experiments were conducted to determine the appropriate strength, duration and frequency of the elctrical impulses applied to the rat gastrocnemius. The voltage was set randomly between figures of 10.5 and 25 volts. A sequence of increasing frequencies ranging from 15 to 100 Hz. were matched with each of the various voltage levels and tested with impulse duration periods of 2 and 5 msec. It was determined that the best tetanic responses in rat gastrocnemius were developed using an electrical stimulation of 25 volts with a frequency of 50 Hz. and impulse duration of 5 msec. Therefore all activated experiments conducted in this thesis incorporated this level of supra-maximal stimulation.

f) The Maintenance of the Muscle

During testing, the muscle electrodes and force transducer were immersed in one litre (L.) of oxygenated bicarbonated-buffered Krebs-

FIGURE 5:

Block diagram of apparatus used for recording and display


STIMULATOR
DISPLACEMENT
TRANSDUCER
MUSCLE
CATHODE RAY
OSCILLOSCOPE
FORCE
TRANSDUCER
STRAIN GAUGE
AMPLIFIER
FILTER
2
1
3
VISUAL DISPLAY
TECA UNIT
UV RECORDER

Ringer's solution at 16.5°C. to 17.8°C., with a pH of 7.3. The solution was pre-made in eight litre quantities consisting of: NaCl, 116.8mM./L.; $NaHCO_3$, 28 mM./L.; $CaCl_2$, 2.5 mM./L..; $MgSO_4$, 3.1 mM./L.; KCl, 3.5 mM./L.; KH_2PO_4, 1.2 mM./L.; and glucose, 11.1 mM./L. (Bahler et al., 1968). The pH was checked before ach experiment while oxygenation (95% O_2, 5% CO_2) commenced one half hour before and continued throughout the period of testing.

ii) Histological and Histochemical Technique

Histological and histochemical studies were performed on one sedentary and one denervated muscle. The muscle tissues used for the histological studies were fixed, dehydrated in increasing concentrations of alcohol, and impregnated by paraffin dispensed by the vacuum infiltrator and parafin dispenser[6]. Sections were cut from the wax blocks on a microtome[7] before being placed in a 37°C. water bath[8] for easy slide pickup. The slides and their accompanying tissue were dried and then stained by the appropriate procedure. The results of the staining techniques were recorded on 35mm. coloured film by the use of a photomicroscope[10].

The apparatus used for the histochemical studies consisted of liquid nitrogen for quick freezing of the tissue, a cryostat[11] for

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6 Model 224, Vacuum Infiltrator and Paraffin Dispenser, Lipsan Manufacturing Company, Detroit, U.S.A.

7 Model 820, Microtome, American Optical Company, U.S.A.

8 Tissuemat Water Bath, Fisher Scientific Company, U.S.A.

9 Model 66632, Slide Warmer, Precision Scientific Company, Chicago, U.S.A.

10 Photomicroscope II, Carl Zeiss, Oberkochen, West Germany.

11 Model CTC, Cryostat International Equipment Company, Needham Heights, U.S.A.

sectioning of frozen tissue at -20°C., and a metabolic incubator[12] for incubation of natural metabolic cycles resulting in the subsequent uptake of the staining material. Recording of the stained results was performed by the use of the photomicroscope.

iii) Recording of Data

The values for the rat's body and muscle weights were recorded by means of a Triple beam balance[13] and Sartorius balance[14] respectively. The muscle lengths were measured to the nearest millimeter on a centimeter ruler between the superior patellar surface of the femur and the plantar surface of the calcaneus.

Data from the strain gauge amplifier, displacement transducer and stimulator were recorded permanently on Kodak linagraph direct print ultraviolet recording paper (Type 2022). All sets of recordings were accompanied by the appropriate calibration figures. An instantaneous recording was made of the force output for each contraction on a storage cathode ray oscilloscope[15]. These recordings were used for visual estimations and subsequently were removed before the next contraction.

The histological and histochemical data was preserved on 35 mm. coloured Kodak film.

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[12] Model 17AD-5, Dubnoff Metabolic Shaking Incubator, Precision Scientific, Subsiduary of GCA Corporation, Chicago, Illinois, U.S.A.

[13] Model 700, Triple Beam Balance, Ohaus Scale Corporation, Florham Park, N.J., U.S.A.

[14] Model 2463, Sartorius Balance, Sartorius-Werke, Gottingen, West Germany.

[15] Model 141B, Cathode Ray Oscilloscope, Hewett and Packard, U.S.A.

C. PROCEDURES

i) Training and Denervation of Rats

The training program consisted of three half hour workouts a week on an inclined treadmill at speeds ranging from 1/4 and increasing to one mile per hour (TABLE 2). On or about the first of each month the incline was increased by five degrees until a slope of thirty degrees was reached. Slope increases accompanyed by increased speeds of running were used to localize the effects of training on the gastrocnemius. Once the required maximal slope and speeds of training were attained, they were maintained until the conclusion of experimentation on the trained groups.

Denervation was performed on November 2nd and 3rd, 1974, one month before experiments commenced. The animals were anesthestized with intraperitoneal sodium pentobarbital, 5 mg. per 100 gm. of body weight. After removal of surface hair on the right leg, an incision was made posterior to and longitudinally with the tibia. The muscle tissue was then separated along the septum between the bicep femoris and the gracilis exposing the popliteal fossa which accomodates the gastrocnemius. Towards the superior end of the poplitea fossa the sciatic nerve divides into two terminal branches, the tibial and common peroneal nerves (Wells, 1966). Upon exposure of this division, a 0.5 cm. section of the tibial nerve was removed to produce the desired denervated effect on the gastrocnemius and soleus muscles. There was one exception to this procedure which was partly due to the inexperience of the investigator. On that occasion the common peroneal nerve was sectioned resulting in denervation of the anterior dorsi flexor muscles.

When the nerve sections were removed a cream antibiotic (neosporan) was applied to the skin and the incision was closed using chromic 4-0

TABLE 2:

EXERCISE PROGRAM FOR THE TRAINED GROUPS OF RATS

MONTH	DATES	SPEED (M.P.H.)	DURATION (MIN.)	ELEVATION (DEGREES)
MAY	3,5,8,10 12,15,17, 19,22,24, 26,29,31	1/4 1/2 1/4	2 26 2	0
JUNE	3,5,7,10 12,14,17, 19,21,24, 26,28	1/4 1/2 1/4	2 26 2	5
JULY	1,3,5,8, 10,12,15, 17,19,22, 24,26,29, 31	1/2 1	25 5	10
AUGUST	5,7,9,12, 14,16,19, 21,23,26, 28,30	1/2 1	25 5	15
SEPTEMBER	2,4,6,9, 11,13,16, 18,20,23, 25,27,30	1/2 1	25 5	20
OCTOBER	2,4,7,9, 11,14,16, 18,21,23, 25,28,30	1/2 1	25 5	25
NOVEMBER	1,4,6,8, 11,13,15, 18,20,22, 25,37,29	1/2 1	5 25	30

(continued . . .)

Table 2 (cont'd)

Exercise Program for the Trained Groups of Rats

MONTH	DATES	SPEED (M.P.H.)	DURATION (MIN.)	ELEVATION (DEGREES)
DECEMBER	2,4,6,9, 10.13.16, 18,20,23, 25,27,30	1/2 1	5 25	30
JANUARY	1,3,6,8, 10,13,15, 17,20,22, .24,27,29,31	1/2 1	5 25	30
FEBRUARY	3	1/2 1	5 25	30

dissolvable suture. A daily vigilance was required with periodic applications of a powder antibiotic (cicatrin) to ensure full recovery.

Due to an epidemic of pneumonia and later technical problems, which were beyond the control of the investigator, the denervation procedure had to be repeated March 1st, 1975. At that time three rats of identical age and breeding as the original groups were denervated and used at the appropriate time in the F/L study. The mentioned epidemic occurred in November, 1974, killing nine of the original 32 rats of which six of the dead were from the denervated groups. Two rats from the trained F/V group were tested even though they were suffering the effects of pneumonia. It appeared that the denervation operation weakened the animals to the point where they were less resistant to a disease introduced close after such an operation.

ii) Preparation of Muscles for the Mechanical Experiments

The testing program is indicated in TABLE 3. At the appropriate time individual rats were removed from the cages, weighed and killed using ethyl ether anhydrous. The skin from the surrounding area of the right leg was removed exposing the underlying musculature. The biceps femoris and gracillis muscle sheaths were dissected away leaving the gastrocnemius unobstructed. An incision was made between the gastrocnemius and the tibia which freed the gastrocnemius and severed the soleus muscle. The femur shaft was then exposed by removing the surrounding musculature. Using a scalpel, the patellar, cruciate and collateral ligaments were severed freeing the superior ends of the tibia and fibula, while the inferior end of the tibiofibular unit was disconnected at the calcaneal facet by the use of bone snips. The tibiofibular unit was then removed while the metatarsal bones were dissected away leaving the intact calcaneous

and muscle tendon. Once the insertion of the gastrocnemius was freed, the shaft of the femur was cut at a point one centimeter superior to the patellar surface. The gastrocnemius, accompanied by its intact origin and insertion bones was immersed in oxygenated ringer's solution where the patella and any remaining unnecessary musculature was removed. A pin was then passed down the femoral shaft and forced through the intercondylar fossa of the patellar surface. This hole was enlarged using a small pointed file to allow easy passage of the force transducer stud.

iii) Collection of Mechanical Data

a) Force-Velocity Data

Preparations were made to allow immediate placement of muscle into the apparatus before dissection. Calibaration figures were taken to confirm linearity of the galvanometer output from the force transducer. These figures were acquired by applying forces to the force transducer stud at 100 gm. increments using an Ohaus spring scale (Model 8001). Depending upon the type of muscle tested (ie., denervated or trained), the strain gauge amplifier was set to produce a full range of deflection of the galvanometer representing force in response to muscle contraction. When these preparations were completed with the commencement of oxygenation of the ringer's solution, dissection procedures followed.

After the hole was made through the patellar surface of the femure, the calcaneus was lodged securely in the jeweller's watch clasp (PLATE 1). Initially every muscle tested in the F/V study was secured in the apparatus without the presence of the added series compliance. When the muscle was secured, the ringer's solution bath was lifted into place, immersing the muscle while the horizontal arm of the support platform was raised to produce a pretension of approximately 10% of maximum force output (Bahler

TABLE 3:

TESTING PROGRAM

DATE	RAT IDENTITY	GROUP	STUDY
DECEMBER 2	1 (S)	SEDENTARY	F/V
DECEMBER 17	1 (D)	DENERVATED	F/V
	2 (D)	DENERVATED	F/V
DECEMBER 19	3 (D)	DENERVATED	F/V
	6 (D)	DENERVATED (ANTERIOR MUSCLE)	F/V
DECEMBER 24	2 (S)	SEDENTARY	F/V
	1 (T)	TRAINED	F/V
	1 (S)	SEDENTARY	F/L
DECEMBER 26	3 (S)	SEDENTARY	F/V
	2 (T)	TRAINED	F/V
	2 (S)	SEDENTARY	F/L
JANUARY 7	4 (S)	SEDENTARY	F/V
	3 (T)	TRAINED	F/V
JANUARY 9	5 (S)	SEDENTARY	F/V
	4 (T)	TRAINED	F/V
JANUARY 14	4 (D)	DENERVATED	F/V
	5 (D)	DENERVATED	F/V
JANUARY 16	5 (T)	TRAINED	F/V
	1 (T)	TRAINED	F/L
JANUARY 21	6 (T)	TRAINED	F/V
	2 (T)	TRAINED	F/L
FEBRUARY 25	3 (S)	SEDENTARY	F/L
	4 (S)	SEDENTARY	F/L
APRIL 1	1 (D)	DENERVATED	F/L
MAY 1	2 (D)	DENERVATED	F/L
	3 (D)	DENERVATED	F/L

et al., 1968). From previous experimentation, estimates of maximum force for each group were obtained and used to determine the approximate 10% pretension levels. Some fluctuations in the pretension levels were necessary to produce subsequent generation of maximal force generation. The electrodes were then immersed in the ringer's bath and placed in contact on either side of the muscle.

Two to four isometric contractions were performed and recorded without the addition of a series compliance. After each contraction the polarity of the electrodes were changed to reduce the effects of polarization. Upon completion of the contraction, where no compliance was incorporated, the pretension was eliminated and the electrodes removed. At this time the overlapping wire loop was rotated to release the watch clasp and calcaneous from the securing chain. The added series spring was hooked to the watch clasp while the horizontal support arm was raised. When the increased height of the support arm accomodated the added length due to the spring, the free end of the spring was hooked into the lowest link of the dangling chain. The 10% pertension level was then sought while the electrodes were placed into position. Two to four contractions were made with the added series compliance in place. Again the polarity of the electrodes was changed after each contraction and the results recorded on the ultraviolet recorder.

This procedure was repeated as many times as the muscle fatigue allowed, that is, when the maximum force output dropped to about 50% of the initial sequence of contractions. The number of contractions performed was partially controlled by the comparability of the force outputs between the two types of contractions.

Throughout the period of experimentation 95% O_2 and 5% CO_2 were

bubbled into the ringer's solution, while the pretension levels of the two types of contractions were fluctuated around the estimated 10% of-maximum-force-output level to facilitate the highest force production.

The procedure was identical for every muscle studied in the F/V experiments. Only the pretension and the strain gauge amplification levels were altered to accomodate the specific characteristics of each of the experimental groups.

When the force level of contraction reached approximately 50% of the initial sequence of contractions, the muscle was removed from the apparatus, weighed and its length recorded. Preparations were then made for the next experiment.

b) Force-Length Data

Preparations of the apparatus for the F/L study were similar to those performed for the F/V experiments. Calibration figures for force were acquired before each experiment using the same technique as in the F/V study. Additional calibration figures were obtained for the displacement transducer. These were acquired by measuring consecutive 0.7 mm. increases in drum displacement on a fixed protractor and recording the galvanometer response on the ultraviolet recorder (PLATE 2). Linearity of the displacement output was verified by measuring the displacement of the line printouts for each angle. When linearity was confirmed for both the force and displacement transducer outputs, oxygenation of the ringer's solution commenced. Dissection proceeded after the body weight of the rat was recorded.

When the dissection procedure was completed with the hole in the patellar surface of the femur being made, the calcaneus was clamped securely in the F/L support strap. The support strap and the accompanying muscle

was placed in the apparatus with the femur being positioned on the force transducer rod and secured by a nut. The free end of the support strap was clamped on the displacement drum where most of the slack was taken up before clamping. The displacement drum was moved eccentrically to obtain a visual estimate of the loacation of the resting length (L_o) using the first indication of force production recorded on the oscilloscope. Stimulation was not necessary to determine L_o becuase the position of the initial increase of static force has been classically accepted as indicative of L_o's position, the displacement drum was moved concentrically 3.5 mm. and experimentation commenced.

At eccentric length increases of 0.7 mm., recordings were made of the static force level followed by a recording of the stimulated or active force production at the same length. Recordings were made of both static and active forces during consecutive length increases up to a maximum of 814 mm. beyond L_o. Due to differences in the F/L characteristics of the PEC's of the three experimental groups, this maximal extension was not always reached. Upon completion of a full range of muscle lengths, the muscle was removed from the apparatus, weighed and its length recorded.

This procedure was strictly followed for every muscle tested. Only the level of amplification of the force transducer output was changed to facilitate a full scale galvanometer response to the different maximal force levels of the various experimental groups.

iv) Collection of Histological and Histochemical Data

a) Histological Data

Histology techniques differed from those of histochemistry in that they involved longer periods of time between dissection and mounting

of the specimen, that is histology involves the use of dead tissue. For this reason a fixative was necessary to preserve the size, shape and protoplasm of the tissue studied. Therefore, fixing fluids act as preservatives and thus inhibit autolytic changes and bacterial growth (Leeson and Leeson, 1970).

The most common reagents employed as fixing agents are formalin, alcohol, mercuric bichloride, potassium bichromate and certain acids (piric, acetic, or osmic) (Leeson and Leeson, 1970). No single fixative possesses these compounds and remains effective. Therefore a fixative was selected using set criteria: 1) the particular tissue or component studied and 2) the staining method used. For these reasons Bouin's fluid was selected to enable study of the connective tissue composition of muscle tissues using Mallory triple stain.

A cross-sectional tissue segment was taken from the posterior portion of the gastrocnemius muscle belly of both a sedentary and denervated rat. Each section was divided, one was immersed and fixed in Bouin's fluid for a period of four hours, while the other portion was instantly frozen and stored for the histochemical study.

The fixed tissue was first washed to remove excess fixative and then dehydrated by passing it through increasing strengths of alcohol (TABLE 4). The tissue was cleaned by removing the dehydrating agent and replacing it with a substance which was miscible with both the dehydrating and embedding agents. The miscible fluid used was toluene. The cleaning agent was progressively infiltrated by paraffin using increasing quantities until the tissue was immersed in 100% of the embedding material. The embedding material was then allowed to solidify around the tissue to form a block. Once in the solid state, the tisse was sectioned and stained.

The tissue blocks were individually placed in a microtome where cross-sectional sections 6 - 10 μ thick were cut. Before the sections were placed on slides, they were put in a water bath of 37°C. while a small amount of egg albumen was smeared on the slide. The albumen provided an adhesive between the sections and slides, and the water bath partially melted the paraffin which further enhanced adhesion. Once the tissue sections were in place the slides were dried on the slide warmer.

The purpose of staining is to enhance natural contrasts while making more evident the various cell and tissue components on an intrinsic material (Leeson and Leeson, 1970). Therefore, before staining was performed, the foreign material had to be removed and the tissue returned to a relatively natural state (TABLE 4). Thus, a paraffin solvent, xylene, was used to deparaffinize the sections. A hydration procedure, using decreasing concentrations of alcohol, was followed to remove the solvent and return the tissue to a distilled water level. The slides were then placed in the Mallory triple stain for six minutes to enhance connective tissue contrast in the sections. After six minutes the slides and tissue sections were placed in running tap water for five minutes to remove excess staining material and then returned to distilled water. To preserve the tissue sections for future use, the slides progressed through another dehydration sequence of alcohols to remove any remaining water. The sections and slides were cleaned using xylene and then mounted. Mounting requires the use of an adhesive substance which has similar refractive index to glass. In these studies, Canada balsam was applied to the sections before being covered by a cover slip. Photographs were then taken using a photomicroscope at magnifications of 31, 125 and 500.

This procedure was followed for tissue sections taken from both

TABLE 4:

FIXATION, EMBEDDING AND STAINING PROCEDURES

(After Davenport, 1960, p. 246)

(A) Fixation and Embedding

I) Fixing time in Bouin's fluid -- 4 hours
II) Wash in running water for 1 hour
III) Transfer to 50% ethyl alcohol for 1 hour
IV) Transfer to 70% alcohol for 1 hour
V) Transfer to 95% alcohol for 1 hour
VI) Transfer to absolute alcohol for 30 minutes
VII) Transfer to toluene (2 changes), 30 minutes each
VIII) Transfer to melted paraffin (2 changes, 30 minutes each
IX) Embed in paraffin to produce block.

(B) Staining

I) Deparaffinize tissue sections in xylene for 2 minutes, repeat twice
II) Blot to remove excess xylene
III) Transfer to absolute alcohol for 30 seconds
IV) Transfer to 90% alcohol for 30 seconds
V) Transfer to 70% alcohol for 30 seconds
VI) Transfer to 50% alcohol for 30 seconds
VII) Transfer to distilled water for 1 minute
VIII) Transfer to Mallory triple stain for 6 minutes
IX) Move to running tap water for 5 minutes
X) Transfer to distilled water for 1 minute
XI) Dip in 50% alcohol
XII) Dip in 70% alcohol
XIII) Dip in 90% alcohol
XIV) Transfer to 100% alcohol for 30 seconds
XV) Blot to remove excess alcohol
XVI) Dip in xylene
XVII) Mount.

the sedentary and denervated muscles.

b) Histochemical Data

The histochemical procedure used involved the use of the mitochondrial enzyme succinate dehydrogenase to indicate fibre type. As the name suggests a dehydrogenase oxidizes a substrate by removing and passing hydrogen to a suitable acceptor. By employing neotetrazolium chloride, this hydrogen transport system was replaced resulting in a blue colouring effect to any Krebs cycle activity. Darker blue or high concentrations of blue depicted a red fibre, with decreasing amounts indicating intermediate to white fibres.

Histochemical techniques involve live tissue and subsequently immediate processing. The frozen muscle sections of both experimental muscles were mounted on cryostat cutting plates and placed in the cryostat at -20°C. In turn the sedentary and denervated muscle tissues were sectioned and placed on slides. The tissue sections were allowed to melt and dry at room temperature to provide some adhesion to the slides.

The fresh sections were then incubated at 37°C. in the presence of: 1) a substrate to be oxidized, 2) a hydrogen acceptor, 3) an enzyme activator and 4) a tetrazolium salt which acted as the trapping agent for the released hydrogen (Chayen, Bitensky, Batcher and Poulter, 1969).

The actual reaction medium used consisted of:

1) 0.1 gm. neotetrazolium chloride (or nitro-blue tetrazolium),
2) 100 ml. of phosphate buffer (of glycyl glycine) at pH 7.8 and,
3) 1.36 gm. of sodium succinate (6 H_2O) giving a 0.05 M solution.

(Chayen et al., 1969)

The sections remained in the incubator for 30 minutes and were then removed. Slides and tissue sections were washed in distilled water, and the egg albumen and a cover slide were applied. Photographs were taken at a microscope magnification of 125 and 500.

v) Analysis of Mechanical Data

a) Theoretical Basis of the Analysis

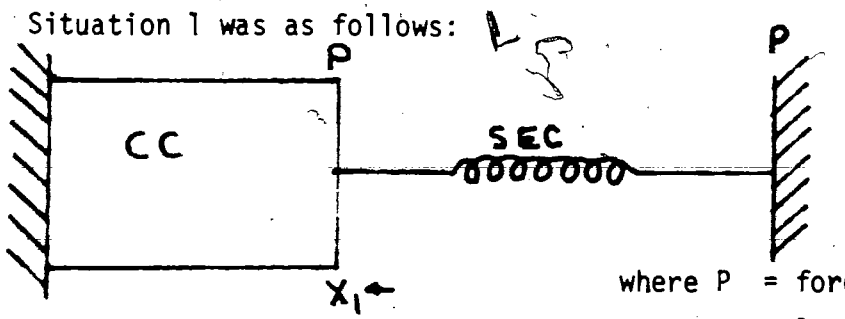
Both methods of analysis required the use of an added compliance in series with the muscle for half of the isometric contractions of every muscle tested. Therefore the data collected from all the F/V experiments were analyzed using both methods.

1) MacPherson's Non-linear Technique

The sole assumption made by MacPherson (1953) was that the velocity of shortening of the CC at any moment was a function only of force at that moment. Furthermore, it has been found that when isometric lengths are less than or equal to the rest length (L_o), the effects of the PEC are neglected (Bahler, 1967). It was found that when the isometric length was greater than L_o the force produced by the PEC was subtracted because it was a passive force which was constant at that length.

The system of analysis was determined in two parts: the first situation without, and the second with an added compliance.

Situation 1 was as follows:



where P = force developed by CC
x_1 = length of the SEC
t = duration of contraction

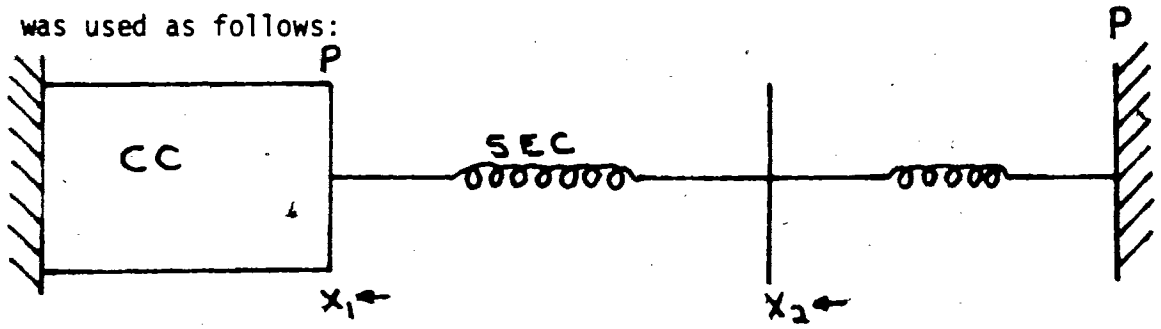
From Hill's model (Equation 1):

$$\left(\frac{dP}{dt}\right)_o = \left(\frac{dP}{dx_1}\right)_o \cdot \left(\frac{dx_1}{dt}\right)_o$$

the velocity of contraction of the CC was determined by rearrangement as follows:

$$\left(\frac{dx_1}{dt}\right)_o = \left(\frac{dP}{dt}\right)_o \cdot \left(\frac{dx_1}{dP}\right)_o \quad \ldots\ldots\ldots\ldots \quad (4)$$

Here the subscript "o" denotes the contraction without added compliance when compliance was added (Situation 2) the subscript "c" was used as follows:



where x_2 = length of the added compliance

which gave $$\left(\frac{dP}{dt}\right)_c = \left(\frac{dP}{d(x_1+x_2)}\right)_c \cdot \left(\frac{d(x_1+x_2)}{dt}\right)_c$$

In this situation the total shortening produced by the CC was the sum of the extensions of both series elastic elements. Therefore, the velocity of shortening of the CC was denoted by:

$$\left(\frac{d(x_1+x_2)}{dt}\right)_c = \left(\frac{d(x_1+x_2)}{dP}\right)_c \cdot \left(\frac{dP}{dt}\right)_c \quad \ldots\ldots \quad (5)$$

Since the velocity of shortening depended only on the force, the values for velocity for any given force (P) in each situation were equated. Thus combination of equations (4) and (5) resulted in:

$$\left(\frac{dP}{dt}\right)_o \cdot \left(\frac{dx_1}{dP}\right)_o = \left(\frac{dP}{dt}\right)_c \cdot \left(\frac{d(x_1+x_2)}{dP}\right)_c \quad \ldots \quad (6)$$

where the compliance of the SEC $\left(\frac{dx}{dP}\right)_1$ was found and written as:

$$\frac{dx}{dP}_1 = \left(\frac{dx}{dP}\right)_c \cdot \left(\frac{dP}{dt}\right)_c \Big/ \left[\left(\frac{dP}{dt}\right)_o - \left(\frac{dP}{dt}\right)_c\right] \quad \ldots (7)$$

The only difference between the contractions was the addition of an added series compliance in Situation 2. Therefore, at the same value of force (P), the compliance of the SEC $\frac{dx}{dP}_1$ was the same for each situation while the discrepancy between the recorded myograms was only due to the E/F characteristics of the added compliance.

Graphic representation of the compliance-force (C_1/F) relationship of the SEC gave an indication of the effects of the experimental conditions on the SEC's mechanical properties. Integration of this relationship with respect to force produced the E/F curve of the SEC and thus resulted in the classic relationship used to describe the properties of the SEC.

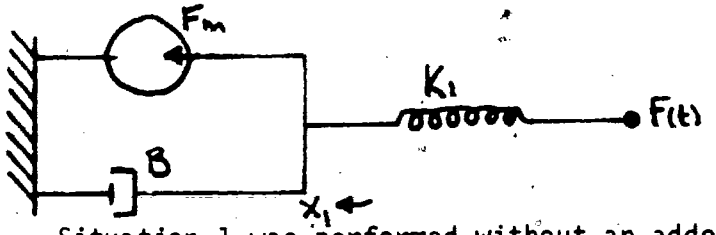
Substituion of the various values of $\frac{dx}{dP}_1$ with their corresponding forces (P) into equation (4) resulted in the calculation of the velocity of the contraction of the CC for each muscle tested (Appendix 1). Finally, these values of force and velocity were plotted to produce the F/V relationship for isometric contractions at a specific length for each muscle.

When the F/V, C_1/F and E/F curves were obtained using this method fo analysis, a comparison was made with the generalized linear analysis of Houk's model by manipulating the same group of isometric myograms. Once this comparison was obtained, the effects of denervation and training were assessed using these particular mechanical parameters.

2) Houk's Linear Technique

The system of analysis was similar to MacPherson's in that it required the use of an added compliance on half the myograms obtained

from each muscle. Houk (1963) made the assumption that the force generator (Fm) switched on instantaneously in the form of a step function. The experimental situations were identical to MacPherson's where one contraction was performed with an added compliance and one without as follows:



Situation 1 was performed without an added compliance where Fm represented the instantaneous force generator, B was a viscous damper, x_1 indicated the length of the SEC, while K_1 represented the inverse of compliance of the SEC and the force produced with respect to time was F (t).

From the definitions,

$$Fm - B\frac{dx_1}{dt} = K_1 x_1 = F(t) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (8)$$

$$\text{where } \frac{dx_1}{dt} = \frac{1}{K_1} \cdot \frac{dF(t)}{dt}$$

Therefore, the substitution of this value of $\frac{dx_1}{dt}$ into equation (8) resulted in:

$$Fm - \frac{B}{K_1} \cdot \frac{dF(t)}{dt} = F(t) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (9)$$

Assuming that Fm acted as a step function, a Laplace operator was used to solve the equation by substituting $\frac{Fm}{s}$ for Fm, SF(s) for $\frac{dF(t)}{dt}$ and F(s) for F(t) into equation (9) as follows:

$$\frac{Fm}{s} - \frac{B}{K_1} \cdot SF(s) = F(s)$$

$$\text{where } \frac{Fm}{s} = F(s)\ (1 + \frac{B}{K_1} s)$$

which resulted in $F(s) = \frac{Fm\frac{K_1}{B}}{s(s + \frac{K_1}{B})}$ . . . . . (10)

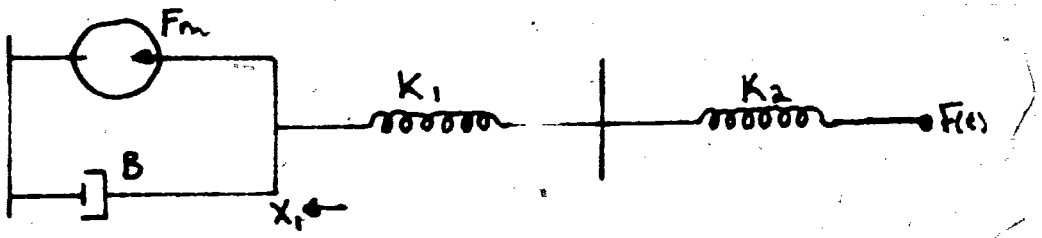
Using the Laplace inverse transform function, $\mathcal{L}^{-1} \frac{1}{s(s + b)} = \frac{1 - e^{-bt}}{- b}$, and making $\frac{1}{s(s + b)}$ equivalent to $\frac{Fm \frac{K_1}{B}}{s(s + \frac{K_1}{B})}$, substitution into equation (10) yielded:

$$F(t) = Fm(1 - e^{\frac{K_1}{B} t}) \quad . . . . . (11)$$

This equation predicts an exponential rise of force with respect to time which has a time constant τ_o which is equal to $\frac{B}{K_1}$; ie.,

$$\tau_o = \frac{B}{K_1} \quad . . . . . (12)$$

The subscript "o" denoted the situation with no added compliance. The subscript "c" denoted the second situation with an added compliance as follows:



where a known added compliance K_2 was placed in series with the muscle model. In this case, equation (8) can be modified as follows:

$$Fm - B \frac{d}{dt} (x_1 + x_2) = \left(\frac{K_1 K_2}{K_1 + K_2}\right) \cdot x = F(t)$$

and $$\frac{d(x_1 + x_2)}{dt} = \left(\frac{K_1 + K_2}{K_1 K_2}\right) \cdot \frac{dF(t)}{dt}$$

then $$Fm - B \left(\frac{K_1 + K_2}{K_1 K_2}\right) \cdot \frac{dF(t)}{dt} = F(t) \quad . . . . . (13)$$

By making the same assumption as in the first situation, the Laplace operator "s" was used to produce

$$F(s) = \frac{Fm}{s}\left(- B\left(\frac{K_1 + K_2}{K_1 K_2}\right)\right) . SF(s)$$

$$\text{where } F(s) = \frac{Fm \cdot \left[\frac{1}{B\left(\frac{K_1 + K_2}{K_1 K_2}\right)}\right]}{\frac{1}{s\left[s + B\left(\frac{K_1 + K_2}{K_1 K_2}\right)\right]}} \quad \ldots\ldots\ldots\ldots\ldots (14)$$

Incorporating the same Laplace inverse transform function used in the first situation resulted in

$$F(t) = Fm \quad 1 - e^{- \frac{1}{B\frac{K_1 + K_2}{K_1 K_2}} t} \quad \ldots\ldots\ldots\ldots (15)$$

where the time constant (τ_c) was obtained by

$$\tau_c = B\frac{K_1 + K_2}{K_1 K_2} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (16)$$

and the subscript "c" denotes the contraction with the added compliance, the time constant(τ)is defined as the time taken to reach 63.2% of the maximum range of force. Therefore the values of T for experimental conditions, both with and without added compliance, were determined for each myogram and the mean value for each condition was computed for each muscle (Appendix 2).

Using equations (12) and (16), the relationship tetween the two values of τ was used to determine the compliance of the SEC as follows:

$$\frac{\tau_c}{\tau_o} = \frac{K_1 + K_2}{K_2}$$

Therefore the compliance of the SEC (C_1) was obtained from

$$K_1 = \left(\frac{T_c}{T_o} \cdot K_2\right) - K_2 \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (17)$$

where $C_1 = \frac{1}{K_1}$

Knowing K_2, the values found for K_1 were substituted into either equations (12) or (16) to determine B, where B was equal in each equation, as follows:

$B = T_o K_1$ from equation (12)

$B = \frac{K_1}{K_1} \frac{K_2}{\mp} \frac{T_o}{K_2}$ from equation (16)

where B represents the slope of the linear F/V vurve and thus was plotted and compared with the non-linear curve derived for the same data. In addition, the maximum velocity of shortening for the linear model was determined from the maximal force (P_o) and the gradient of the linear F/V relationship as follows:

$$V_{max} = \frac{P_o}{B} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (18)$$

b) Statistical Treatment

Mean values and standard deviations were calculated for body weight, muscle weight and muscle length. The calculations were performed for the muscles used in the F/V and F/L studies as follows:

1) mean values ($\bar{X}$) = $\Sigma x/N$

2) standard deviation (SD) = $\frac{(x - \bar{x})^2}{n - 1}$

where x represented the raw data and N was the number of measurements (Haber and Runyon, 1975).

Analyses of variance were performed on these measures to determine if the differences among the experimental groups were significant (Appendix 8). An F-ratio was determined from these calculations and the level of

significance found by referring to F-ratio tables.

If a significant difference was represented by the F-ratio then an HSD (Honestly significant Difference) test was performed to determine the α-level of significance between the mean values of the individual groups (Haber and Runyon, 1973). A difference between two means was significant at a given α-level if it equalled or exceeded the HSD value which was calculated as follows:

$$HSD = q\alpha \frac{s^2w}{n}$$

where s^2w = within group variance

n = number of observed subjects

$q\alpha$ = constant for a given α-level

(Appendix 8) (Haber and Runyon, 1973).

The same system of statistical analysis was used to determine the level of significance of differences found between measurements obtained for the major experimental conditions in the F/V study. Mean value and standard deviation curves were computed for the F/V and C_1/F relationships for each groups using the following APL program:

```
      ∇DSTAT[⎕]∇
    ∇ DSTAT X;R;MAX;MIN;N;MEAN;VAR;SD;MD;MED;V;M
[1]   SD←(VAR←(+/(X-MEAN←(+/X)÷N)*2)÷(N←⍴X)-1)*0.5
[2]   'MEAN                    ', 6 1 ⍕MEAN
[3]   'STANDARD DEVIATION      ', 5 1 ⍕SD
    ∇
```

(Appendix 4 and 5)

Analyses of variance resulting in the α-levels of significance were limited to the linear mechanical parameters found in the F/V study. Analysis of the corresponding non-linear data was restricted to reading and discussion of the individual relationships.

The F/L study involved only paired subjects in each of the experimental situations. Therefore relevant statistical data could not be obtained beyond mean value relationships (Appendix 6). Thus the mean value curves were analysed by using the maximum force outputs, the shape of each curve and the slope of a tangent drawn to the upper end of the F/L curve of the PEC for each condition.

c) Comparison of the Linear and Non-Linear models

The linear and non-linear F/V relationships of the CC and the C/F, E/F relationship of the SEC were compared visually for all the experimental groups. The aim of this visual assessment was to determine whether any changes in the properties of elements of the linear model reflected those of the non-linear model. It was concluded that if these responses were similar in direction for both models then the statistical analysis performed on the linear perameters could be used to indicate any significant effects due to denervation and/or training.

It has been shown that Houk's linear model demonstrated a linear F/V relationship whose triangular area under-the-curve was identical to the area presented by the non-linear F/V relationship acquired during isotonic contractions (Milhorn, 1966). It should be noted that the point representing maximal force at zero velocity (P_o) was identical for both models in that it was measured and notdeduced indirectly. Therefore it was assumed that a good linear representation of a non-linear mechanical property of either the CC or the SEC would be one that demonstrated the same area under-the-curve. Consequently the linear and non-linear F/V, C/F and E/F relationships of the larger sedentary and trained groups were compared with the theoretical relationships calculated from the application of the above technique.

vi) Analysis of Histological and Histochemical Data

Analysis of histological and histochemical data was restricted to a discussion of mean estimates of muscle fibre, size and type. The histochemical data dealing with connective tissue concentrations will be limited to a discussion of a visual comparison of photographic results obtained from denervated and sedentary muscle sections.

Slides were made for both techniques of muscle sections at microscope magnifications of 31, 125 and 500. When these slides were enlarged to 3.5 x 5 inch photographs, the size of the photographed material was increased by 3.44. Thus enlarging increased the magnification to 134, 430 and 1720 respectively.

Estimates of size and diameter for a number of the three types of muscle fibre found in rat gastrocnemius were made in millimeters from the 134 and 430 magnified histological photographs. The millimeter measurements were then convertes to microns (μ) to indicate the actual size of the fibres as they are found in the muscle.

The estimates of fibre composition were made from the same histological photographs. Fibre size and degree of staining were used as the criteria to distinguish between red, white and intermediate fibres. A series of one inch squares were drawn on one photograph of both the denervated and the sedentary sections. Within each square the numbers of the three fibre types were counted and tabulated. Mean values for each of the fibre types were determined from the photographs of sections of both the denervated and sedentary muscles. The results of this analysis are examined in the DISCUSSION.

CHAPTER IV

RESULTS

The purpose of this study was to assess the effects of both denervation and training on the mechanical properties of linear and non-linear models of isolated rat gastrocnemius muscle. The data obtained also allowed assessment of the degree to which changes in linear properties reflected changes in the non-linear properties. Anatomical, histological and histochemical examinations were made in order to quantify the effects of both denervation and restricted use on the structural components of muscle. Such examinations were made in order that the mechanical changes could be interpreted physiologically.

A. ANATOMICAL MEASUREMENTS

The means and standard deviations of body weight (BW), muscle weight (MW) and muscle length (ML) were calculated with respect to each experimental group (TABLE 5). Analysis of Variance (ANOV) was performed in order to determine the effects of the experimental treatments on BW, MW, and ML (Appendix 8).

i) Body Weight

An F value of 0.406 was obtained for the ANOV of BW (TABLE 6, Appendix 8). This indicated that the experimental treatments had no significant effect on BW.

ii) Muscle Weight

The ANOV for MW was performed in two parts. The first part determined if there were any significant differences among muscle weights

TABLE 5:

MEANS AND STANDARD DEVIATIONS OF ANATOMICAL MEASURES

GROUP	RAT NO.	F/L SUB-GROUP	STUDY	BODY WT. (BW) (gm.wt.)	$\overline{BW}$ MEAN±SD (gm.wt.)	MUSCLE WT. (MW) (gm.wt.)	$\overline{MW}$ MEAN±SD (gm.wt.)	MUSCLE L. $\overline{ML}$ (cm.)	$\overline{ML}$ MEAN±SD (cm.)
DENERVATED									
1 month	1		F/V	593.8		3.0760		5.3	
	2		F/V	668.7		3.1662	2.9669	5.4	5.6
	3		F/V	709.0		2.9710	±0.1931	5.9	±0.25
	1	1	F/L	602.4		2.6546		5.8	
2 months	4		F/V	617.0	623.4	2.2362		5.8	
	5		F/V	634.1	± 49.5	2.4167	2.2467	5.8	
	2	2	F/L	585.3		1.9340	±0.1953	5.7	5.8
	3		F/L	544.3		2.4074		5.8	
	*6		F/V	655.6		4.6913		4.8	±0.05
SEDENTARY									
	1		F/V	656.3		5.0391		5.2	
	2		F/V	765.9		4.9247		5.3	
	3		F/V	698.3		4.6900		5.2	
	4		F/V	705.0		5.1427		5.3	
	5		F/V	612.4	631.9 ± 71.6	4.8281	4.9617 ±0.1598		5.23 ±0.05
	1	1	F/L	521.0		4.9963		5.2	
	2		F/L	547.1		5.0602		5.2	
	3	2	F/L	583.6		5.1338		5.2	
	4		F/L	597.7		4.8407		5.2	
TRAINED									
	'1		F/V	774.8		5.6387		5.2	
	'2		F/V	579.9		5.4672		5.2	
	3		F/V	678.1		5.6544		5.3	
	4		F/V	662.6	652.8	5.8803	5.4894	5.2	5.2
	5		F/V	700.0	± 72.5	5.6790	±0.3029	5.3	±0.08
	6		F/V	683.7		5.5158		5.1	
	1	1	F/L	579.5		5.2530		5.2	
	2		F/L	563.9		4.8271		5.1	

* Anterior muscles were denervated and tested one month after denervation.

' These rats were tested while suffering the effects of pneumonia for a one month period.

TABLE 6:

MEAN DIFFERENCES FOR BODY WEIGHT

GROUP	DENERVATED 623.4 gm. wt.	SEDENTARY 631.9 gm. wt.	TRAINED 652.8.gm. wt.
DENERVATED 623.4 gm. wt.	---	8.5*	29.4*
SEDENTARY 631.9 gm. wt.	---	---	20.9*
TRAINED 652.8 gm. wt.	---	---	---

* Not Significant

of the sedentary, trained and denervated (one month) groups. The second part was performed on muscle weights of both denervated groups (one month and two months) and the sedentary group. This procedure was necessary to assess significant differences between muscle weights of each denervated group (one month vs. two months) as well as among the denervated (one month), trained and sedentary groups.

ANOV for MW in part one produced an F value of 141.07 which indicates that there were significant differences present among the three groups (Appendix 8). Interpretation of F by way of the HSD method resulted in the determination of significant differences tetween the mean muscle weights of each pair of the three groups at the α-level of 0.01 (TABLE 7).

An ANOV applied to part two (denervated one and two months and sedentary groups) showed an F value of 351.0143 which indicated a significant difference among muscle weights of the groups (for group mean differences see TABLE 7). In fact, the HSD method indicated that the differences tween mean muscle weights of each denervated group was significant at the same level (TABLE 7). The greatest difference occurred between the mean muscle weights of the trained and denervated (two months) groups and was also significant at the α-level of 0.01 (TABLE 7).

iii) Muscle Length

The results of ANOV of ML were similar to those found for MW with one exception. The F value of 13.33 indicated significant differences between the muscle lengths of the denervated (one month), sedentary and trained groups (Appendix 8). The individual differences in mean ML between the paired groups indicated no significant difference between the sedentary and trained groups while there was a significant difference between the

denervated (one month) and sedentary groups at the α-level of 0.01 (TABLE 8, Appendix 8). The exception arose when analyzing the differences between the mean muscle lengths of the two denervated groups.

B. THE EFFECTS OF DENERVATION OF MUSCLE STRUCTURE

The estimates of fibre composition of the rat gastrocnemius muscles studies were made using the somewhat arbitrary criteria of fibre size and degree of staining. Red fibres have been found to be rich in mitochondria and thus stain dark, while they are also small in size. On the other hand, white muscle fibres are at least twice the size of red fibres and show insignificant numbers of mitochondria in relation to red fibre content (Gould, 1973). The third type of fibre, intermediate, lies between these distinct types. Using these criteria, the sedentary muscle tissue composition was estimated to be 15.2% red, 55.9% white and 28.8% intermediate (PLATE 6a, TABLE 9). Based on succinate dehydrogenase activity, the gastrocnemius of the denervated animal was composed of a significantly smaller number of white fibres (34%) than the sedentary (55.9%). This reduction in white fibre composition resulted in a supposed increase in the proportion of red fibre (24%) and intermediate fibre (42%) composition (TABLE 9).

Estimates of the fibre size were made from PLATES 6a and 6c (TABLE 9). A better visual indication of the effect of denervation on fibre size is represented at a magnification of 1720 in PLATE 7a (sedentary) and PLATE 7b (denervated). Visual estimates and measurements suggested a 50% reduction in fibre size for both red and intermediate fibre types; while the reduction is size due to denervation exceeded 70% for white fibres (TABLE 9).

TABLE 7:

MEAN DIFFERENCES FOR MUSCLE WEIGHT

GROUP	DENERVATED (1 month) 2.9669 gm.wt.	DENERVATED (2 months) 2.2386 gm.wt.	SEDENTARY 4.9617 gm.wt.	TRAINED 5.4894 gm.wt.
DENERVATED (1 month) 2.9669 gm.wt.	---	0.7183*	1.9948*	2.5225*
DENERVATED (2 months) 2.2486 gm.wt.	---	---	2.7131*	3.2408*
SEDENTARY 4.9617 gm.wt.	---	---	---	0.5277*
TRAINED 5.4894 gm.wt.	---	---	---	---

* Significant at α-level of 0.01 (see Appendix 8)

TABLE 8:

MEAN DIFFERENCES FOR MUSCLE LENGTH

GROUP	DENERVATED (1 month) 5.6 cm.	DENERVATED (2 months) 5.8 cm.	SEDENTARY 5.23 cm.	TRAINED 5.2 cm.
DENERVATED (1 month) 5.6 cm.	---	0.2	0.37*	0.4*
DENERVATED (2 months) 5.8 cm.	---	---	0.57*	0.6*
SEDENTARY 5.23 cm.	---	---	---	0.03
TRAINED 5.2 cm.	---	---	---	---

* Significant at α-level of 0.01 (see Appendix 8)

TABLE 9:

MUSCLE FIBRE COMPOSITION AND SIZE

MUSCLE TYPE	FIBRE COMPOSITION (% TOTAL)			FIBRE SIZE (μ)		
	RED	WHITE	INTERMEDIATE	RED	WHITE	INTERMEDIATE
SEDENTARY	15.2	55.9	28.8	23.2	48.8	30.2
DENERVATED	24.0	34.0	42.0	11.6	16.2	13.9

PLATE 6:

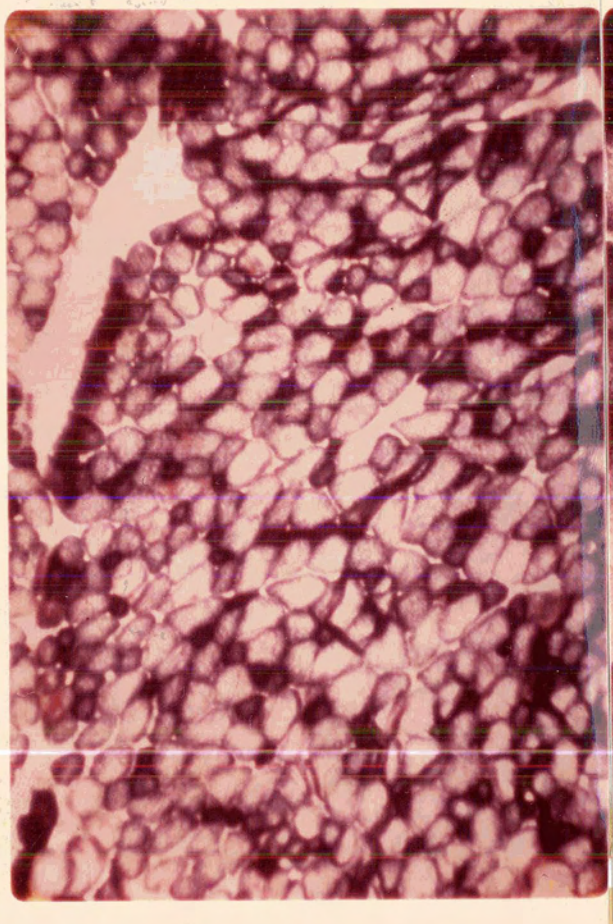
Shown are the results of the histochemical technique involving the mitochondrial enzyme Succinate Dehydrogenase.

a) The types and proportion of muscle fibres in sedentary rat gastrocnemius. Magnification 134x.

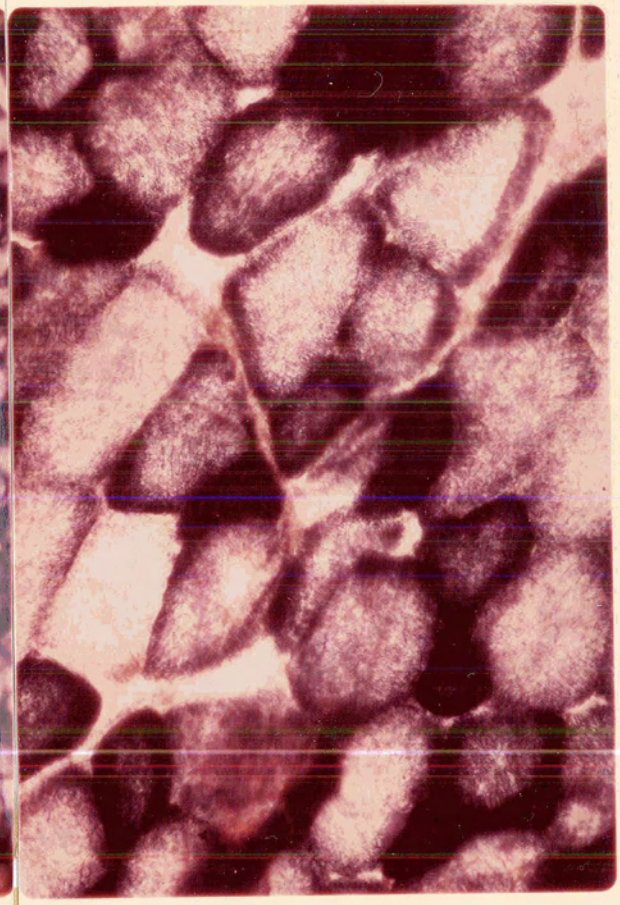
b) Demonstrates the size and type of muscle fibre present in sedentary rat gastrocnemius. Magnification 430x.

c) Shows the reduced size and activity of succinate dehydrogenase in all fibre types present in rat gastrocnemius denervated for two months. Magnification 430x.

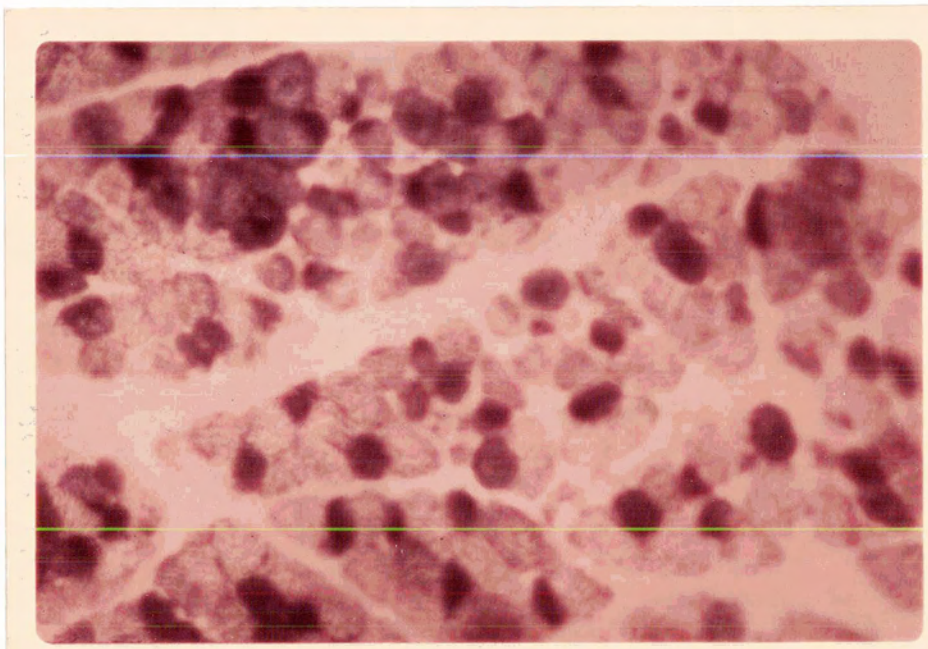
a



b



c



Comparing the denervated tissue with the sedentary tissue at both magnifications indicates decreased mitochondrial activity for all fibres present. This suggests that the aerobic capacities of the muscle were affected by denervation.

The results obtained by histological examination are shown at a magnification of 1720 in PLATES 8a and 8b. The effects of denervation on fibre size are clearly shown in these plates. Although the distinction between fibre types is not present, it is evident that there exists at least a 50% reduction in size of all fibres shown.

The Mallory trichrome stain used for histological examination indicated the presence of any connective tissue by turquoise to blue colour. PLATE 8a, the sedentary tissue section, indicates very little connective tissue between the individual fibres; whereas, the denervated tissue (PLATE 8b) demonstrates a significantly larger amount. This indicates that connective tissue build-up or replacement around the individual fibres has been occurring during the period of denervation.

C. MECHANICAL PROPERTIES OF COMPONENTS OF THE LINEAR AND NON-LINEAR MODELS

The purpose of this section is to compare the effects of denervation, restricted use and training on the mechanical properties of components of linear and non-linear models of muscle. The comparative analysis of non-linear properties was restricted to a visual evaluation and the results are therefore presented as graphic relationships of the properties of the CC and SEC. Statistical evaluation of the linear mechanical parameters was performed and will be presented in the appropriate sections. The mechanical properties of the CC and PEC at different muscle lengths could not be analyzed for both the linear and non-linear models. Therefore,

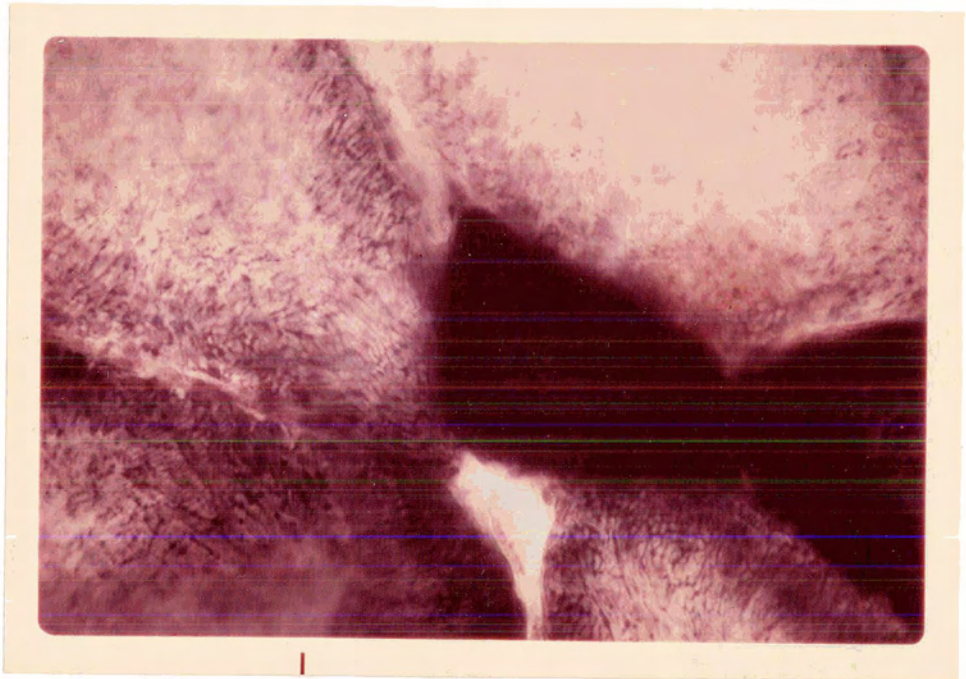
PLATE 7:

The results of histochemical staining at a magnification of 1720x.

a) Shows the size and mitochondrial activity involved with red, white and intermediate muscle fibres in healthy sedentary muscle.

b) Demonstrates the effect of two months of denervation on the size and mitochondrial activity of these muscle fibres.

a



b

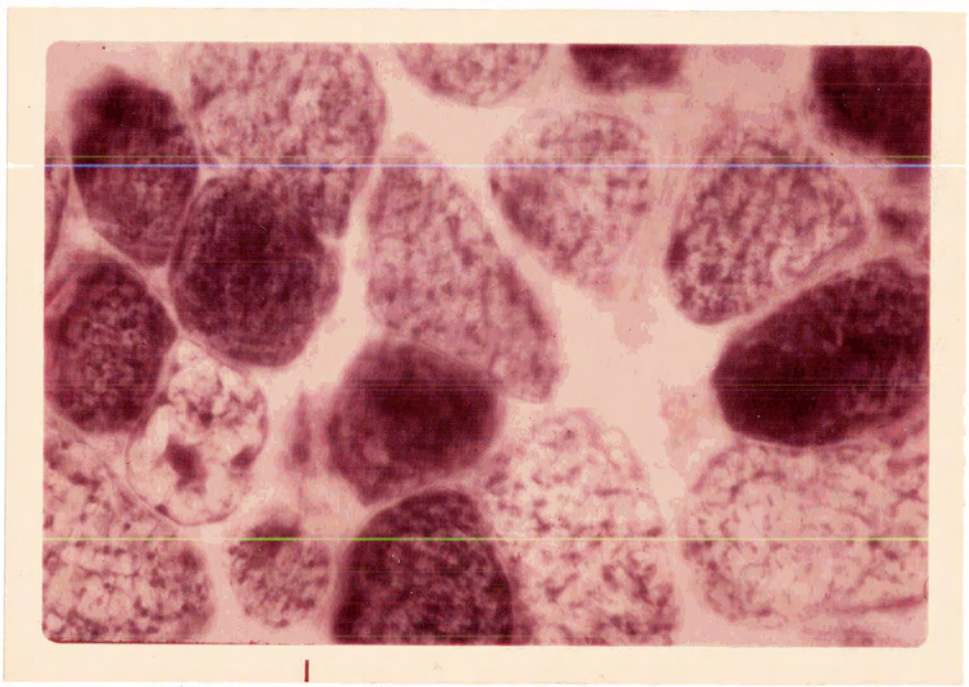


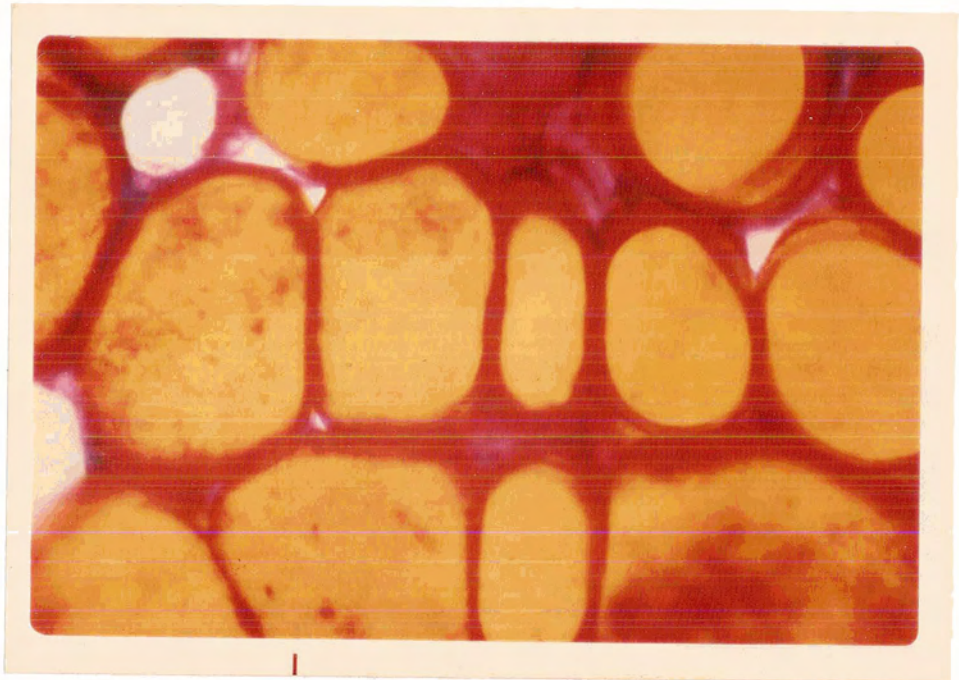
PLATE 8:

The results of the histological technique using mallory trichrome stain to indicate connective tissue.
Connective tissues are turquoise to blue in colour, while muscle fibres are yellow to red.

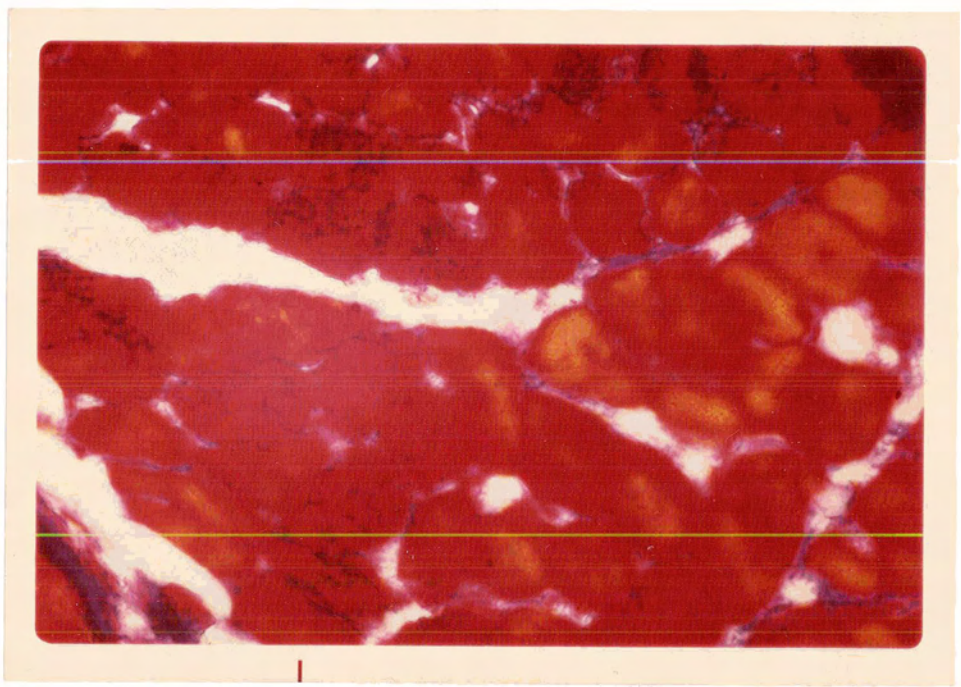
a) Demonstrates the size of muscle fibres but gives no indication of fibre type. Small amounts of connective tissue can be distinguished between some of the fibres. Magnification 1720x.

b) Indicates a definite decrease in fibre size. Much larger amounts of connective tissue can be seen between every fibre shown. Magnification 1720x.

a



b



these properties and the changes due to the experimental treatments were examined using the non-linear model and separate groups of experimental animals. The data obtained from these mechanical experiments is contained in Appendices 1, 2 and 3.

i) The Contractile Components

a) The Force-Velocity Relationships

The linear and non-linear force-velocity (F/V) relationships for the various experimental groups are shown graphically on different scales (for purposes of clarity) in figures 8 to 13. For each group, mean values for velocity were computed at equal increments of force for the non-linear representations of each of the experimental conditions (Appendix 4). These values, along with those mean values (B) calculated for the linear F/V relationship (TABLE 10), were plotted to produce mean values F/V relationships for all conditions tested (Figure 14). The mean values of Figure 14 were reproduced in Figure 15 with the addition of bars representing standard deviations of the means of velocity at any given force. In the latter figure, two experimental sub groups, namely denervated group 3 and trained group 1 were not included. The reasons for this omission were that these groups were not planned, they were not of a statistically acceptable size and they represented treatments which deviated from the experimental conditions tested. Therefore the relationships shown in Figure 15 were the results of those experimental conditons initially planned for this study.

Statistical analysis was performed on the linear F/V relationship obtained from the denervated (group 1), sedentary and trained (group 2) groups. The data obtained from these groups was shown in TABLE 10 and Appendices 4 and 5, and the application of the ANOV to this data is shown

TABLE 10:

MEANS AND STANDARD DEVIATIONS OF LINEAR MECHANICAL PARAMETERS

(See Method of Analysis, Chapter III for Abbreviations)

GROUP	F/V SUB-GROUPS	RAT NO.	To (sec.)	Tc (sec.)	K_1 ($\frac{gm.wt.}{cm.}$)	COMPLIANCE $C=1/K_1$ ($\frac{cm.}{gm.wt.}$)	$\bar{C}$ MEAN±S.D. ($\frac{cm.}{gm.\ wt.}$)
DENERVATED		1	0.0425	0.0548	2894	0.000346	0.000454
(1 month)	1	2	0.0538	0.0652	2119	0.000472	±0.000100
		3	0.0490	0.0580	1837	0.000544	
(2 months)	2	4	0.0474	0.0563	1877	0.000533	0.000509
		5	0.0422	0.0509	2062	0.000485	±0.000034
	3	*6	0.0506	0.0700	3830	0.000261	
SEDENTARY		1	0.0635	0.0909	4315	0.000232	
		2	0.0612	0.0849	3873	0.000258	0.000244
	3	3	0.0602	0.0836	3887	0.000257	±0.000013
		4	0.0560	0.0804	4357	0.000230	
		5	0.0564	0.0798	4149	0.000241	
TRAINED		'1	0.0909	0.1174	2910	0.000344	0.000318
	1	'2	0.0754	0.1011	3410	0.000293	±0.000037
		3	0.0629	0.0803	2766	0.000362	
	2	4	0.0718	0.0951	3245	0.000308	0.000324
		5	0.0580	0.0776	3379	0.000296	±0.000028
		6	0.0643	0.0839	3048	0.000328	

* Anterior muscles were denervated and tested one month after denervation.

' These rats were tested while suffering the effects of pneumonia for a one month period.

GROUP	F/V SUB-GROUPS	RAT NO.	MAXIMUM FORCE -PRETENSION(P_o) (gm.wt.)	P_o MEAN±SD (gm.wt.)	B ($\frac{gm.wt.sec.}{cm.}$)	$\bar{B}$ ($\frac{gm.wt.sec.}{cm.}$)	V ($\frac{cm.}{sec.}$)	$\bar{V}$ MEAN±S.D. ($\frac{cm.}{sec.}$)
DENERVATED		1	192	235	123.08	109.08	1.56	2.21
(1 month)	1	2	282	± 45	144.17	± 15.98	2.47	±0.57
		3	232		90.0		2.60	
(2 months)		4	75	73	88.97	87.99	0.84	0.83
	2	5	71	± 3	87.01	± 1.39	0.82	±0.01
	3	*6	1247		181.25		6.88	
SEDENTARY		1	2615		274.11		9.54	
		2	2600	2668	237.09	244.64	10.46	10.94
	1	3	2480	±170	234.02	±16.95	11.11	±0.98
		4	2934		243.09		12.03	
		5	2711		234.11		11.58	
TRAINED		'1	1800	1758	264.52	260.81	6.80	6.74
	1	'2	1715	± 59	257.10	± 5.25	6.67	±0.08
		3	2240		173.98		12.88	
		4	2867	2560	233.09	199.73	12.30	12.85
	2	5	2400	±290	196.92	±24.55	12.25	±0.79
		6	2734		195.98		12.95	

* Anterior muscles were denervated and tested one month after denervation.

' These rats were tested while suffering the effects of pneumonia for a one month period.

FIGURE 8:

The linear (straight lines) and non-linear force-velocity relationships for rat gastrocnemius denervated one month.

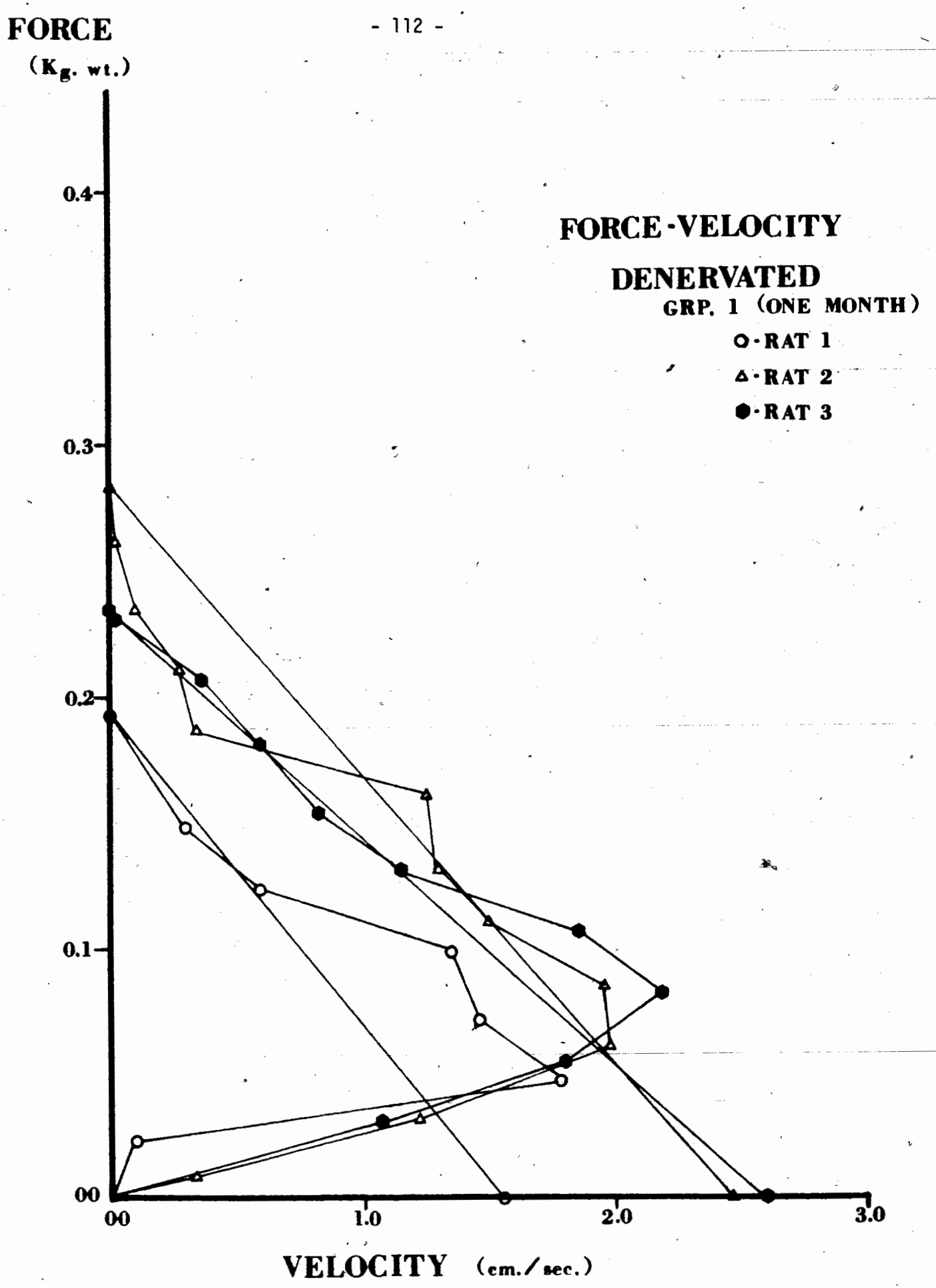

FORCE
(Kg. wt.)
0.4
0.3
0.2
0.1
00
00
1.0
2.0
3.0
VELOCITY (cm./sec.)
FORCE-VELOCITY
DENERVATED
GRP. 1 (ONE MONTH)
O-RAT 1
Δ-RAT 2
⬢-RAT 3

FIGURE 9:

The linear (straight lines) and non-linear force-velocity relationships for rat gastrocnemius denervated for two months.

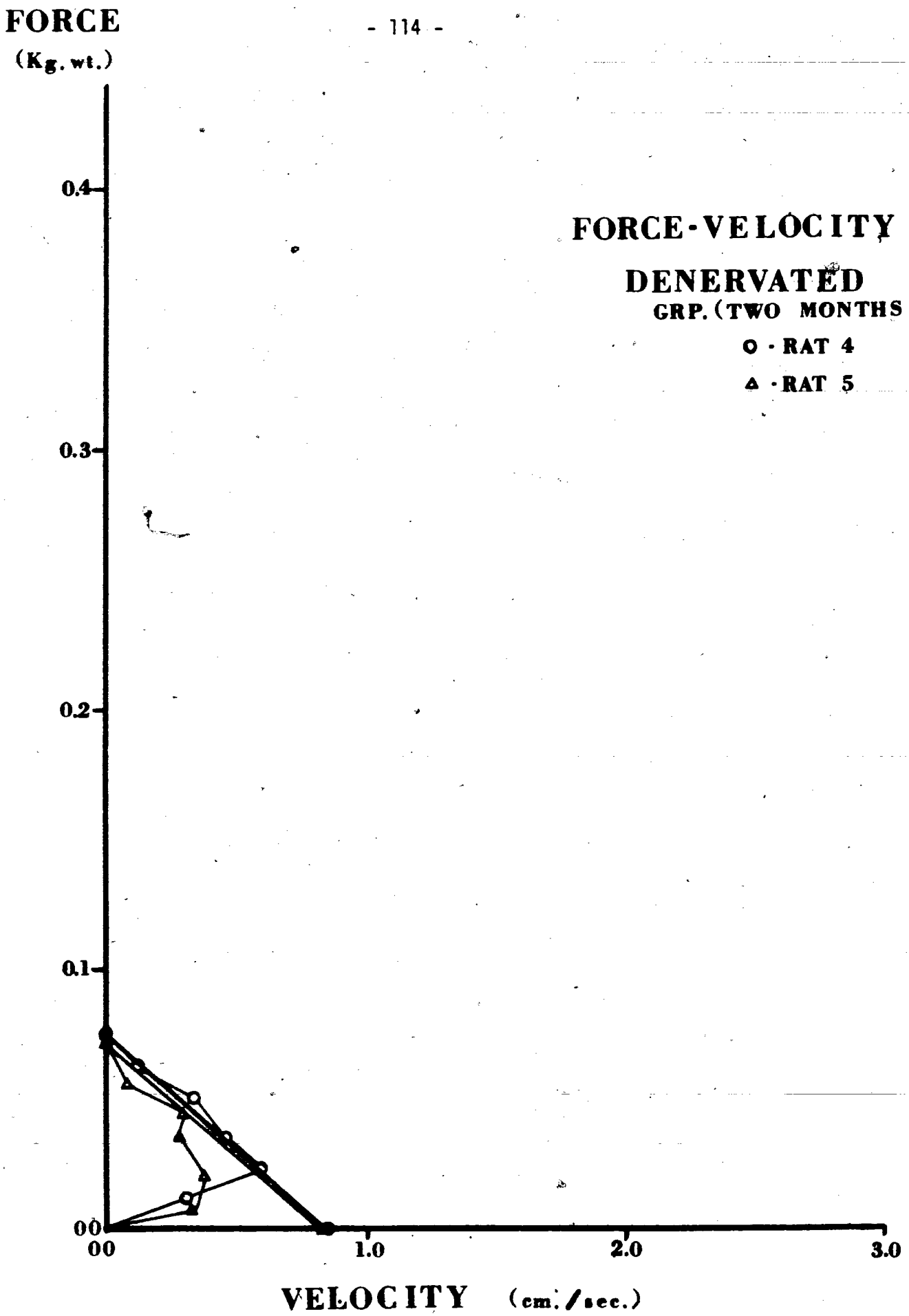

FORCE
(Kg. wt.)
0.4
0.3
0.2
0.1
00
00
1.0
2.0
3.0
VELOCITY (cm./sec.)
FORCE-VELOCITY
DENERVATED
GRP. (TWO MONTHS)
O - RAT 4
Δ - RAT 5

FIGURE 10:

The linear (straight lines) and non-linear force-velocity relationships for rat gastrocnemius when the anterior muscles were denervated one month.

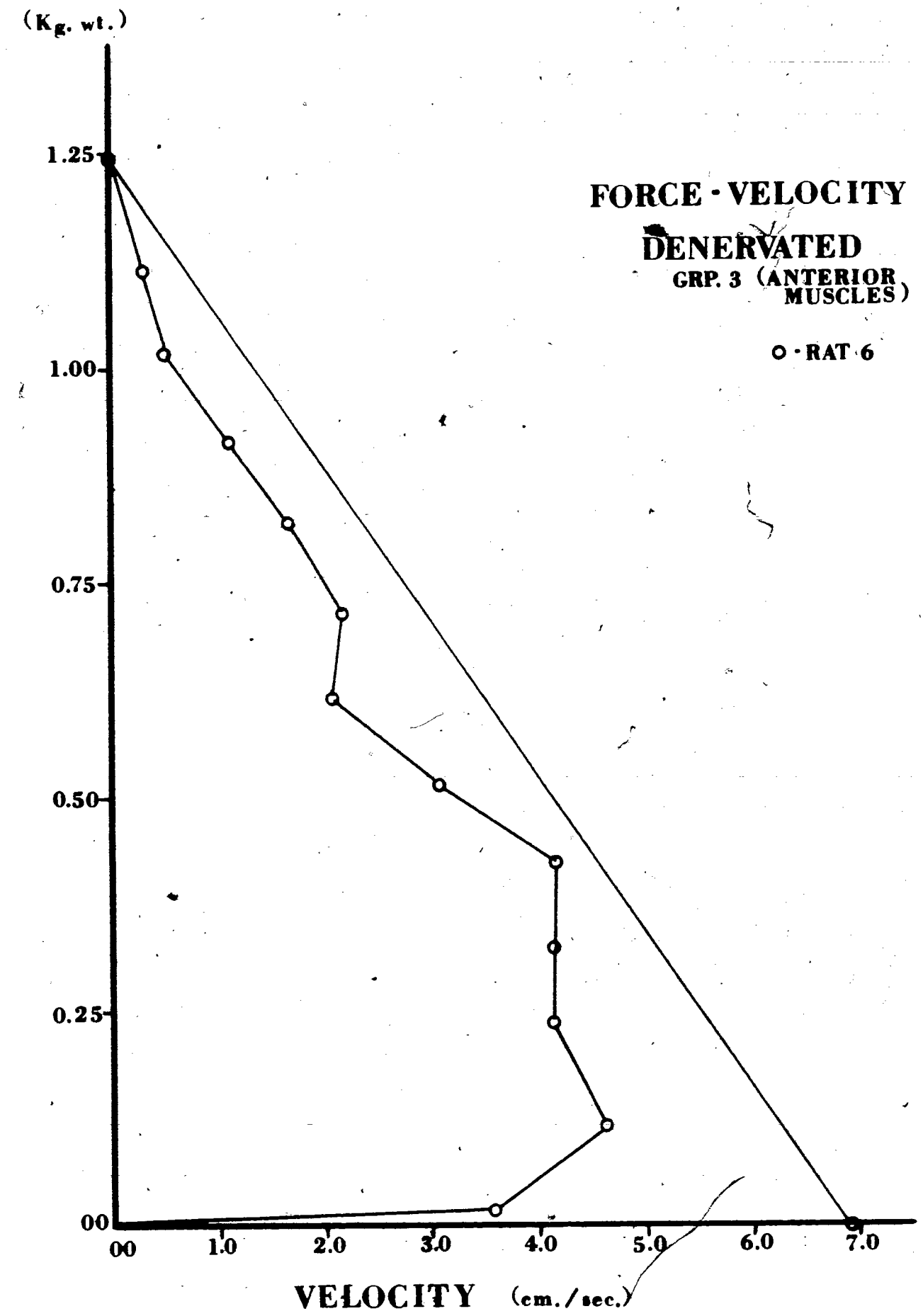

FORCE
(Kg. wt.)
1.25
1.00
0.75
0.50
0.25
00
00
1.0
2.0
3.0
4.0
5.0
6.0
7.0
VELOCITY (cm./sec.)
FORCE - VELOCITY
DENERVATED
GRP. 3 (ANTERIOR MUSCLES)
O - RAT 6

FIGURE 11:

The linear (straight lines) and non-linear force-velocity relationships for sedentary rat gastrocnemius.

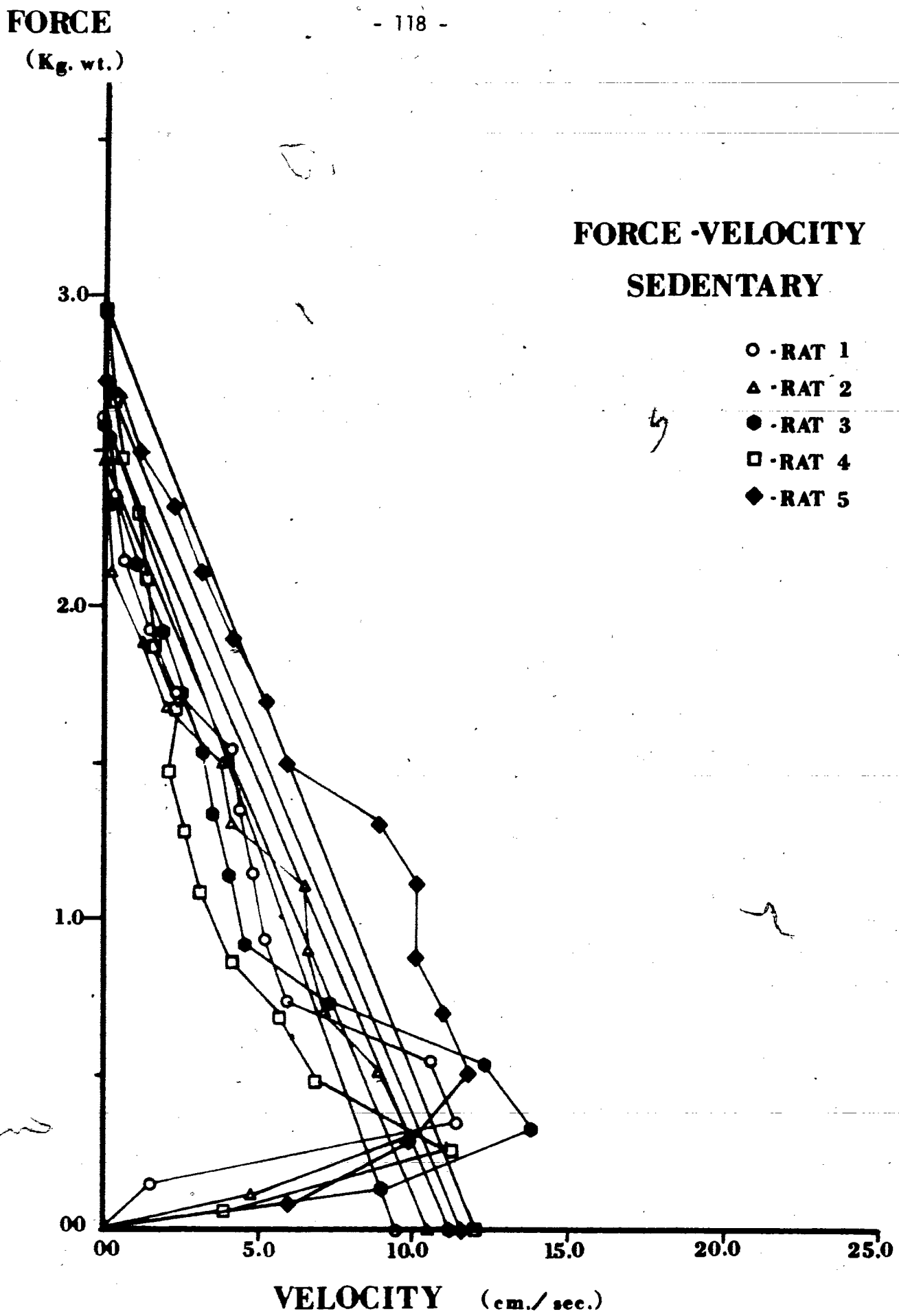
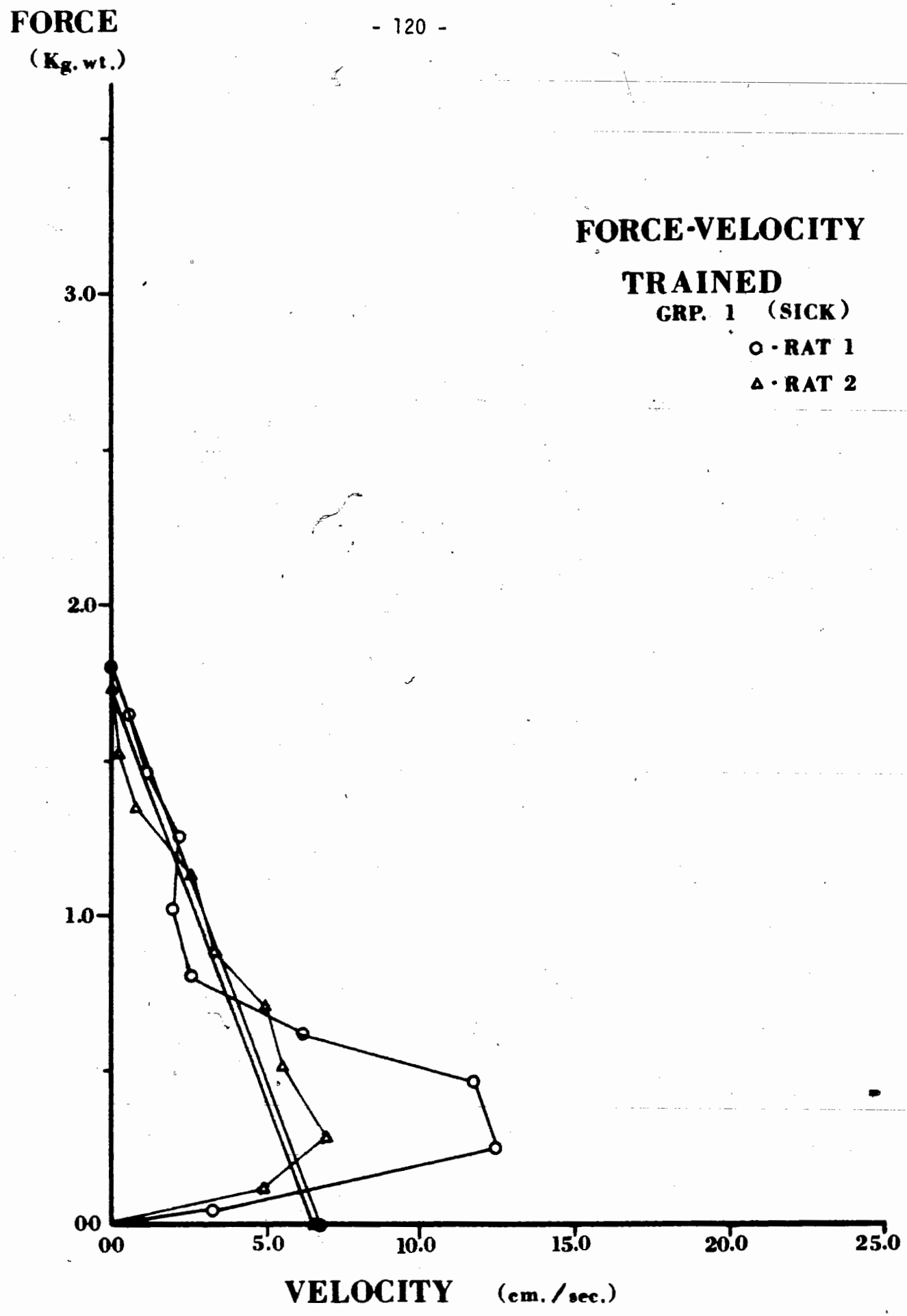

FORCE
(Kg. wt.)
FORCE -VELOCITY
SEDENTARY
○ - RAT 1
△ - RAT 2
● - RAT 3
□ - RAT 4
◆ - RAT 5
3.0
2.0
1.0
00
00
5.0
10.0
15.0
20.0
25.0
VELOCITY (cm./sec.)

FIGURE 12:

The linear (straight lines) and non-linear force velocity relationships for trained rat gastrocnemius when the animal was sick.


FORCE
(Kg. wt.)
FORCE-VELOCITY
TRAINED
GRP. 1 (SICK)
○ - RAT 1
△ - RAT 2
3.0
2.0
1.0
00
00
5.0
10.0
15.0
20.0
25.0
VELOCITY (cm./sec.)

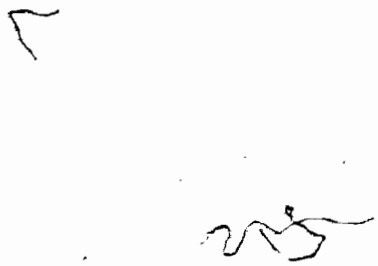


FIGURE 13:

The linear (straight lines) and non-linear force-velocity relationships for trained rat gastrocnemius.

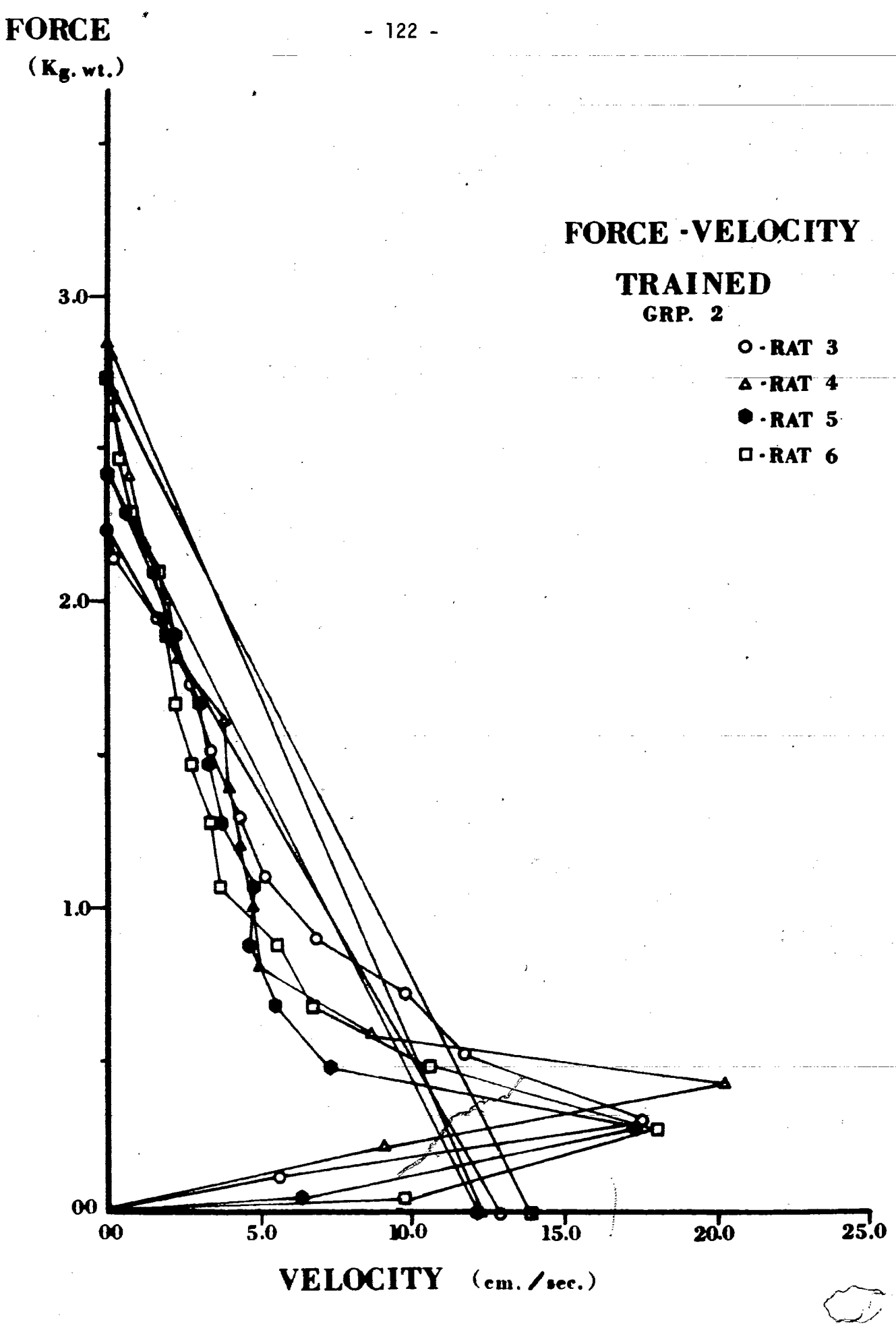

FORCE
(Kg. wt.)
FORCE -VELOCITY
TRAINED
GRP. 2
○ - RAT 3
△ - RAT 4
● - RAT 5
□ - RAT 6
3.0
2.0
1.0
00
00
5.0
10.0
15.0
20.0
25.0
VELOCITY (cm./sec.)

FIGURE 14:

Mean linear (straight lines) and non-linear force-velocity relationships for rat groups presented in FIGURES 8 to 13. Mean velocity values were computed at equal increments of force for each group.

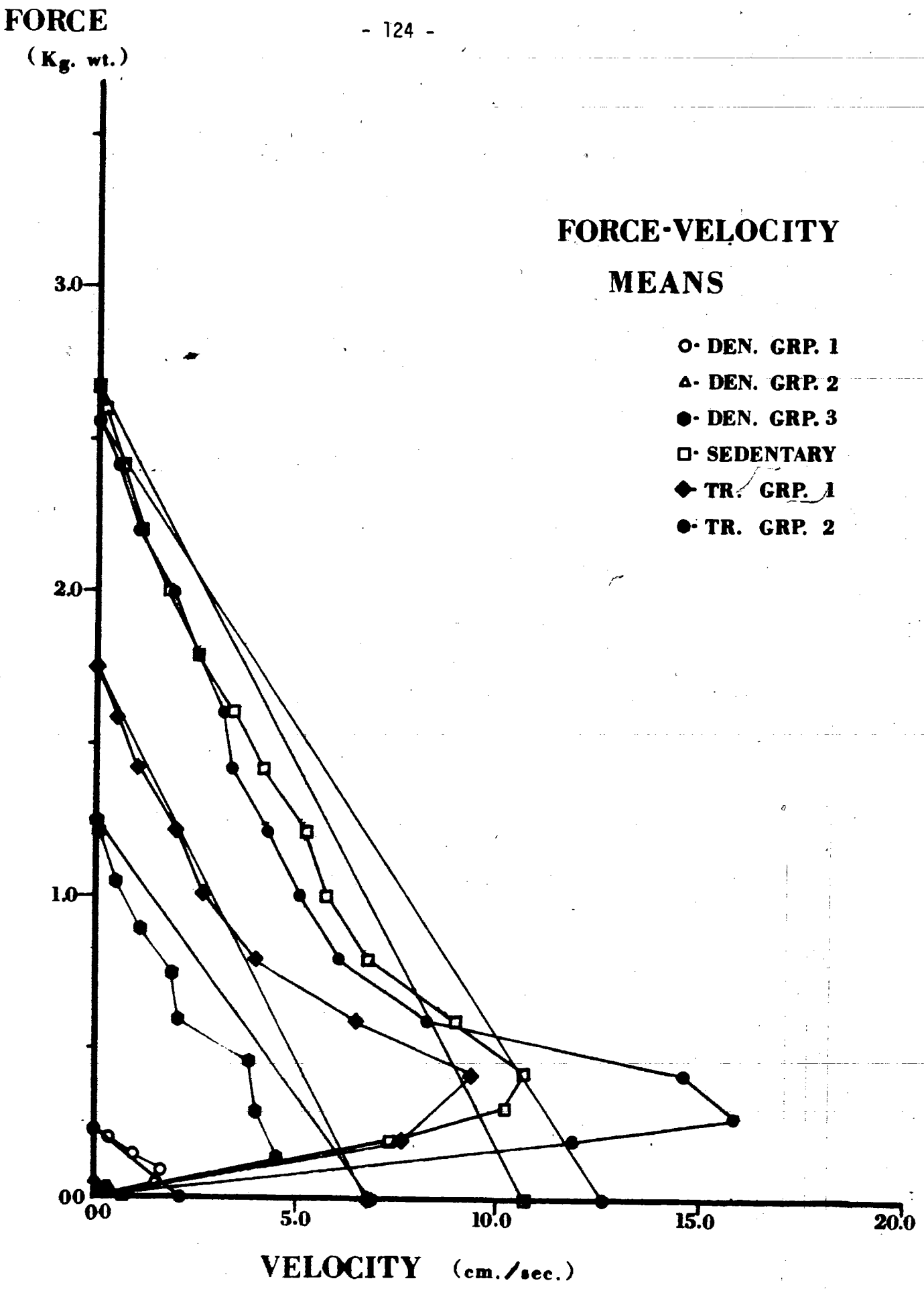
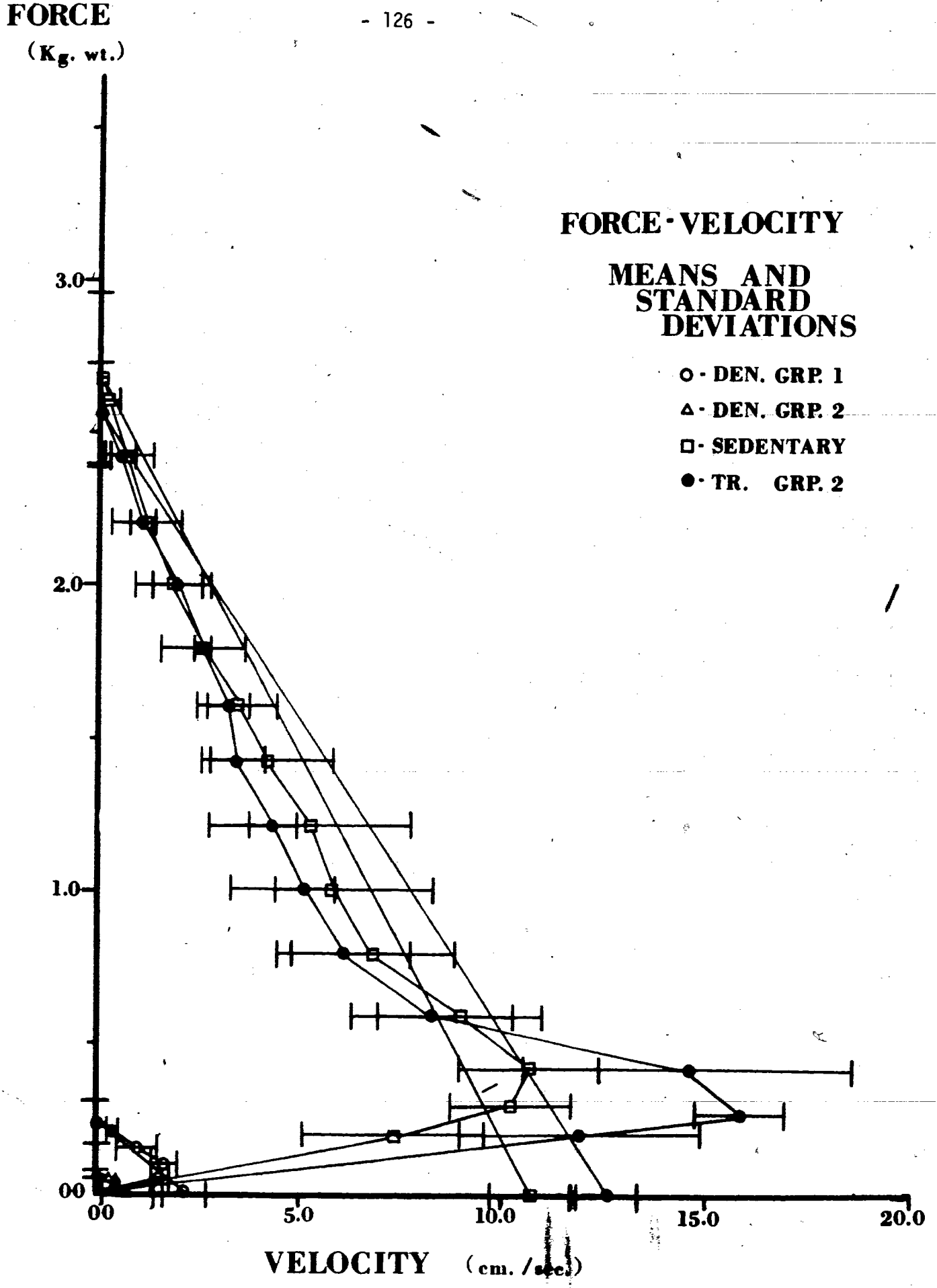

FORCE
(Kg. wt.)
FORCE-VELOCITY
MEANS
DEN. GRP. 1
DEN. GRP. 2
DEN. GRP. 3
SEDENTARY
TR. GRP. 1
TR. GRP. 2
3.0
2.0
1.0
00
00
5.0
10.0
15.0
20.0
VELOCITY (cm./sec.)

FIGURE 15:

Mean and standard deviation linear (straight lines) and non-linear force-velocity curves for the primary experimental groups.


FORCE
(Kg. wt.)
FORCE · VELOCITY
MEANS AND STANDARD DEVIATIONS
○ · DEN. GRP. 1
△ · DEN. GRP. 2
□ · SEDENTARY
● · TR. GRP. 2
3.0
2.0
1.0
00
00
5.0
10.0
15.0
20.0
VELOCITY (cm. / sec.)

in Appendix 9.

The use of statistical analysis was justified by the fact that the slope of each linear F/V relationship was described by a single value (B). Similar statistical procedures were applied to the values of maximal isometric force (P_o) and the theoretical values of maximal velocity (V_{max}). The latter was obtained by dividing the value of P_o (gms. wt.) by the corresponding value of B (gms. wt. sec. $cm.^{-1}$).

The result of the ANOV of the values of B was an F value of 43.88 which indicated a significant difference among the linear F/V relationships of the denervated (group 1), sedentary and trained (group 2) groups (Appendix 9). Application of the HSD method showed that a significant difference between the denervated and sedentary groups existed at the α-level of 0.01 (TABLE 11), while a α-level of significance of 0.05 was present between the sedentary and trained groups. These findings indicated that both experimental conditions produced significant effects on the linear F/V relationship. Both denervation and training resulted in values of B which were lower than that obtained from the sedentary groups; and the greatest reduction in B was due to denervation.

The ability of the muscles to produce isometric force was assessed by performing an ANOV on the values of P_o obtained from the same groups mentioned earlier. An F value of 155.12 was computed which indicated that significant differences existed among the groups (Appendix 9). The individual mean differences between groups were then tested and significant differences between the sedentary group and denervated group, and between the trained group and denervated group were present at the α-level of 0.01, while no significant difference was found between the sedentary and trained groups (TABLE 12). These findings showed that denervation had a significant

TABLE 11:

MEAN DIFFERENCES FOR B

GROUP	DENERVATED (1 month) 109.08 gm.wt.sec./cm.	SEDENTARY 244.64 gm.wt.sec./cm.	TRAINED (group 2) 199.73 gm.wt.sec./cm.
DENERVATED (1 month) 109.08 gm.wt.sec./cm.	---	135.56**	90.65**
SEDENTARY 244.64 gm.wt.sec./cm.	---	---	44.91*
TRAINED (group 2) 199.73 gm.wt.sec./cm.	---	---	---

* Significant at an α-level of 0.05

** Significant at an α-level of 0101 (see Appendix 9).

TABLE 12:

MEAN DIFFERENCE FOR P_o

GROUP	DENERVATED (1 month) 235 gm.wt.	SEDENTARY 2668 gm.wt.	TRAINED (group 2) 2560 gm.wt.
DENERVATED (1 month) 235 gm.wt.	---	2433*	2325*
SEDENTARY 2668 gm.wt.	---	---	108
TRAINED (group 2) 2560 gm.wt.	---	---	---

* Significant at an α-level of 0.01 (see Appendix 9).

effect on maximal force production, whereas training did not.

The point at which the linear F/V relationship crossed the velocity axis represented that theoretical velocity which can be attained at zero force and thus is the maximal velocity (V_{max}) of shortening that can be produced by the muscle. In the previous paragraph it was stated that no significat difference was found between mean values of P_o of the sedentary and trained groups. As there was a difference between the mean values of B of these groups, differences between the mean values of V_{max} and the same groups must be present. As expected, ANOV of V_{max} produced an F value of 153.20 which indicated a significant difference among the three groups (Appendix 9). Further analysis of V_{max} indicated that a significant difference existed between the denervated and sedentary groups and denervated and trained groups at a α-level of 0.01, while the difference between the sedentary and trained groups was also significant but at an α-level of 0.05 (TABLE 13).

In an attempt to assess the effects of denervation and training on the linear and non-linear F/V relationships of the CC, the changes indicated by statistical analysis of the linear F/V relationships required comparison with the graphic representations of the non-linear F/V relationships. Inspection of Figure 14 indicated differences among the non-linear F/V relationships obtained from the various experimental groups. Figure 15 showed that the standard deviations of velocity at a given force did not allow any significant difference to be distinguished between the non-linear F/V relationships of the sedentary and trained groups. The result conflicted with the observation that a significant difference was indicated between the linear F/V relationships (B) of these groups. Conversely, the changes in both linear and non-linear F/V relationships

TABLE 13:

MEAN DIFFERENCES FOR V_{max}

GROUP	DENERVATED (1 month) 2.21 cm./sec.	SEDENTARY 10.94 cm./sec.	TRAINED (group 2) 12.85 cm./sec.
DENERVATED (1 month) 2.21 cm./sec.	---	8.73**	10.64**
SEDENTARY 10.94 cm./sec.	---	---	1.91*
TRAINED (group 2) 12.85 cm./sec.	---	---	---

* Significant at an α-level of 0.05

** Significant at an α-level of 0.01 (see Appendix 9).

which resulted from denervation were obviously great (Figure 15). Comparison of changes in the linear and non-linear F/V relationships due to the experimental treatments are examined in detail in the DISCUSSION.

b) The Isometric Force-Length Relationships

A separate group of rats, receiving the same experimental treatments as in the F/V study, were used to determine the isometric force-length (F/L) relationships of the CC. These rats were indicated in TABLE 6 as being part of the F/L study. The F/L relationships of two denervated and sedentary groups are shown graphically in Figures 16 to 19. Compariosn of the two groups in each condition gave some indication of the effects of prolonged denervation and restricted use on the CC of muscle at different isometric lengths. A third group, trained, is presented in Figure 20 which indicates the effects of a specific type of training on these mechanical properties. The experimental groups were not large enough in numbers for statistical analysis, therefore the analysis was limited to observation of the individual graphs and the resulting mean value curves (Figure 21, Appendix 6). These results were complementary to those described in the previous section, in which the isometric force (P_o) was examined at one length of the muscle in the primary experimental group. The present results substantiated those described previously in that the isometric forces produced throughout a range of lengths by the trained rats were only slightly greater than the equivalent results from the sedentary rats (Figure 21). In fact the changes brought about by training appeared less than those due to a difference of two months in age of the sedentary groups.

TABLE 6 shows that the older rats in the sedentary group (sub group 2) had a greater mean BW although the mean MW was no larger than

FIGURE 16:

The force-length relationship for rat gastrocnemius denervated one month. The interrupted line indicates the tangent corresponding to the approximate linear portion of the mean F/L relationship of the PEC for this group.

The letters CC and PEC denotes the F/L relationships for the contractile component and the parallel elastic component respectively. (SEE LABELLING ON GRAPH)

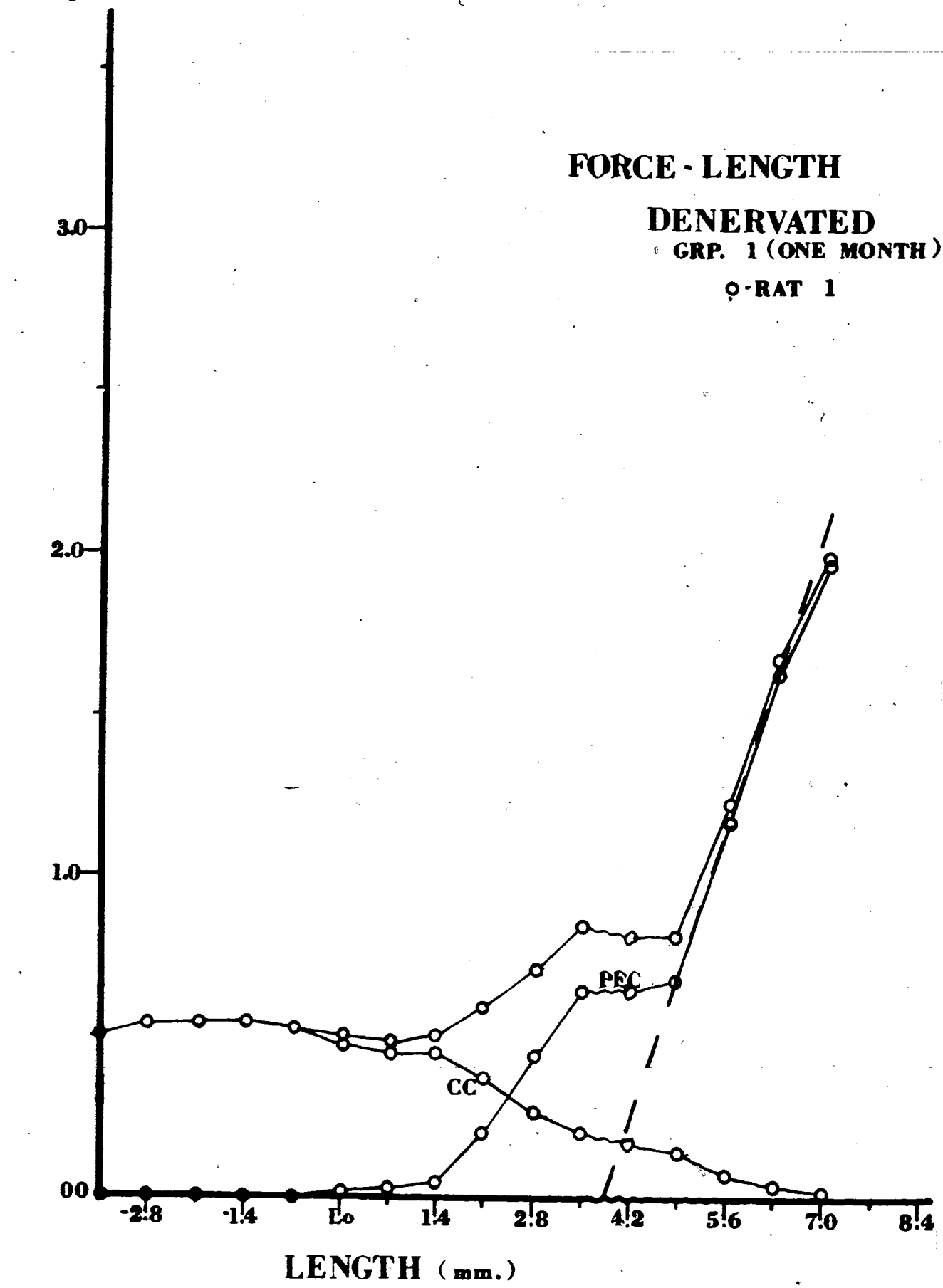

FORCE
(Kg. wt.)
FORCE - LENGTH
DENERVATED
GRP. 1 (ONE MONTH)
♀-RAT 1
3.0
2.0
1.0
00
PEC
CC
-2.8
-1.4
Lo
1.4
2.8
4.2
5.6
7.0
8.4
LENGTH (mm.)

FIGURE 17:

The force-length relationship for rat gastrocnemius denervated two months. The interrupted line indicates the tangent corresponding to the approximate linear portion of the mean F/L relationship for the PEC for this group. (SEE LABELLING ON GRAPH)

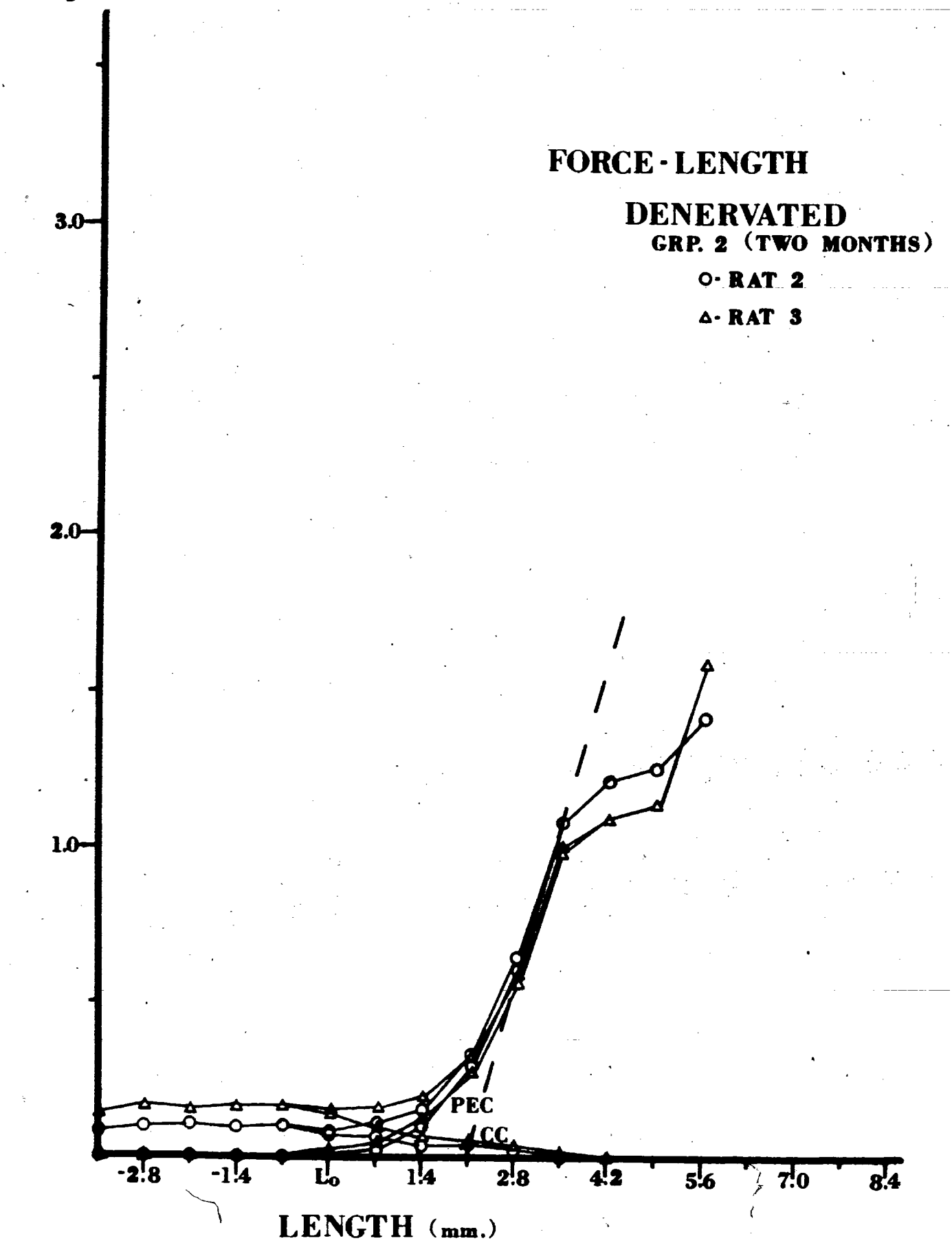

FORCE
(Kg. wt.)
FORCE - LENGTH
DENERVATED
GRP. 2 (TWO MONTHS)
O- RAT 2
Δ- RAT 3
3.0
2.0
1.0
PEC
CC
-2.8
-1.4
Lo
1.4
2.8
4.2
5.6
7.0
8.4
LENGTH (mm.)

FIGURE 18:

The force-length relationship for sedentary rat gastrocnemius. The interrupted line indicates the tangent corresponding to the approximate linear portion of the mean F/L relationship of the PEC for this group. (SEE LABELLING ON GRAPH)

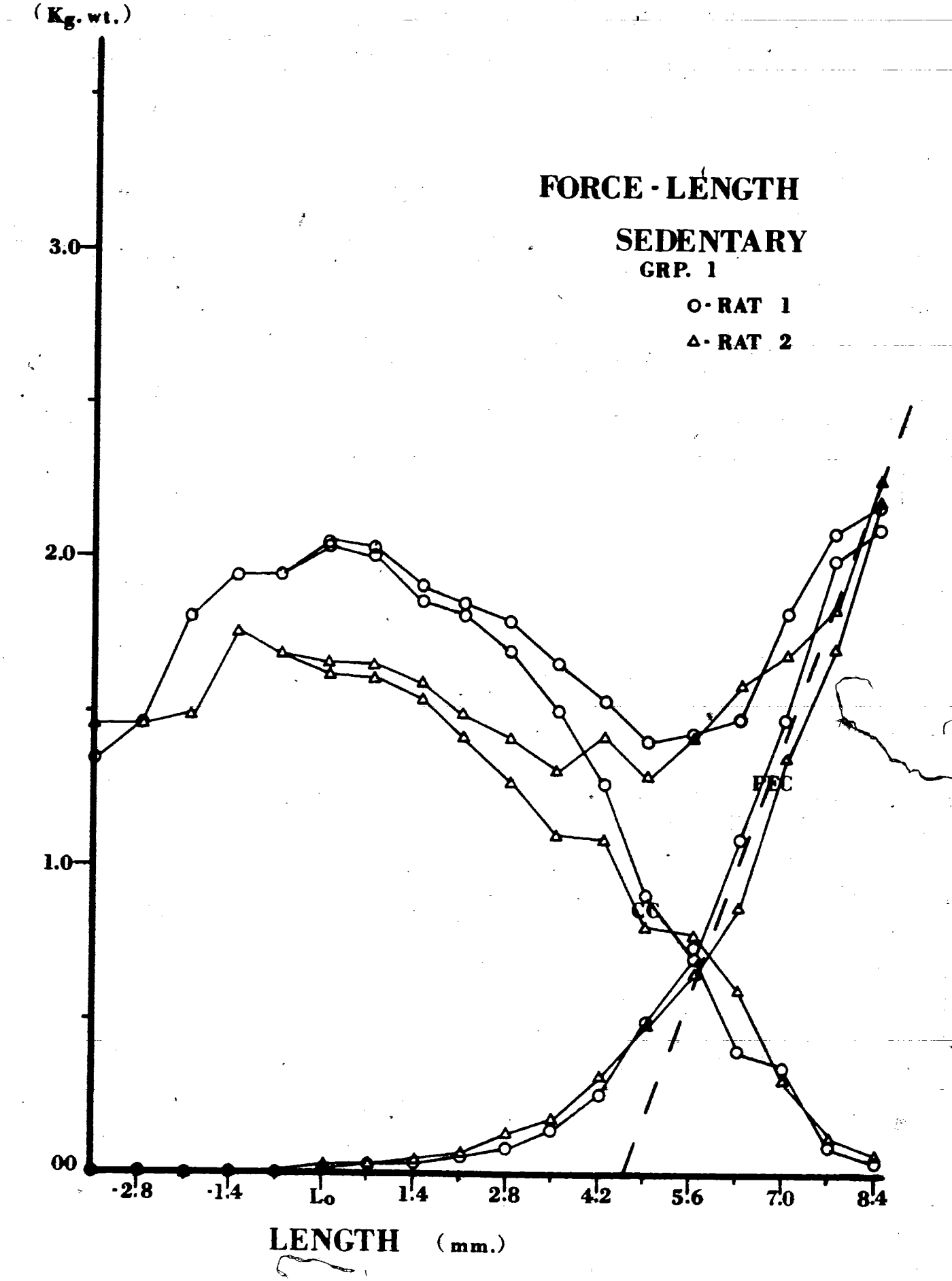

FORCE
(Kg. wt.)
FORCE - LENGTH
SEDENTARY
GRP. 1
O - RAT 1
Δ - RAT 2
3.0
2.0
1.0
00
-2.8
-1.4
Lo
1.4
2.8
4.2
5.6
7.0
8.4
PEC
CC
LENGTH (mm.)

FIGURE 19:

The force-length relationship for sedentary rat gastrocnemius. These animals were two months older than those shown in FIGURE 18. The interrupted line indicates the tangent corresponding to the approximate linear portion of the mean F/L relationship of the PEC for this group. (SEE LABELLING ON GRAPH)

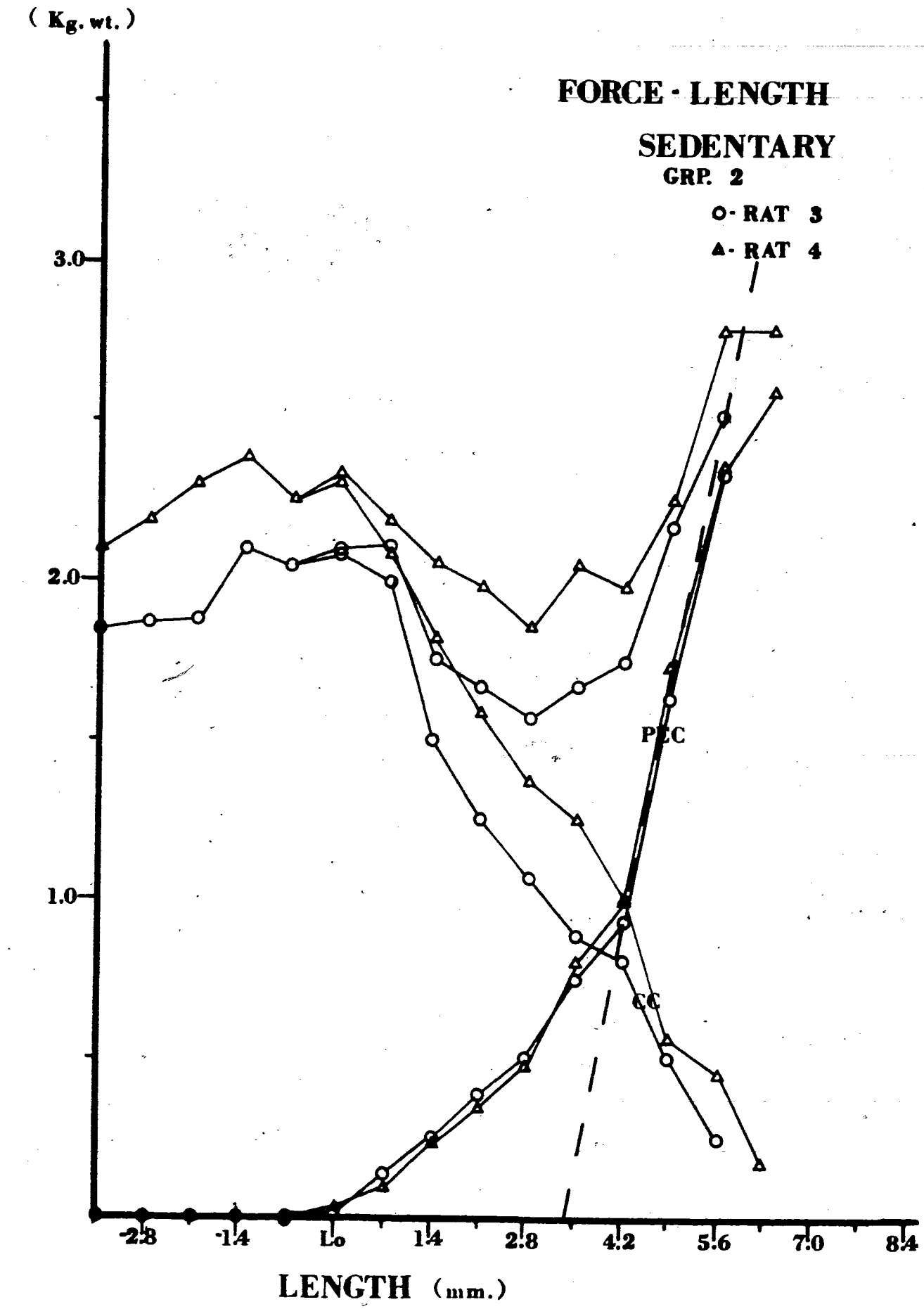

FORCE
(Kg. wt.)
FORCE - LENGTH
SEDENTARY
GRP. 2
O - RAT 3
Δ - RAT 4
3.0
2.0
1.0
PEC
EC
-2.8
-1.4
Lo
1.4
2.8
4.2
5.6
7.0
8.4
LENGTH (mm.)

FIGURE 20:

The force-length relationship for trained rat gastrocnemius. The interrupted line indicates the tangent corresponding to the approximate linear portion of the mean F/L relationship of the PEC for this group. (SEE LABELLING ON GRAPH)

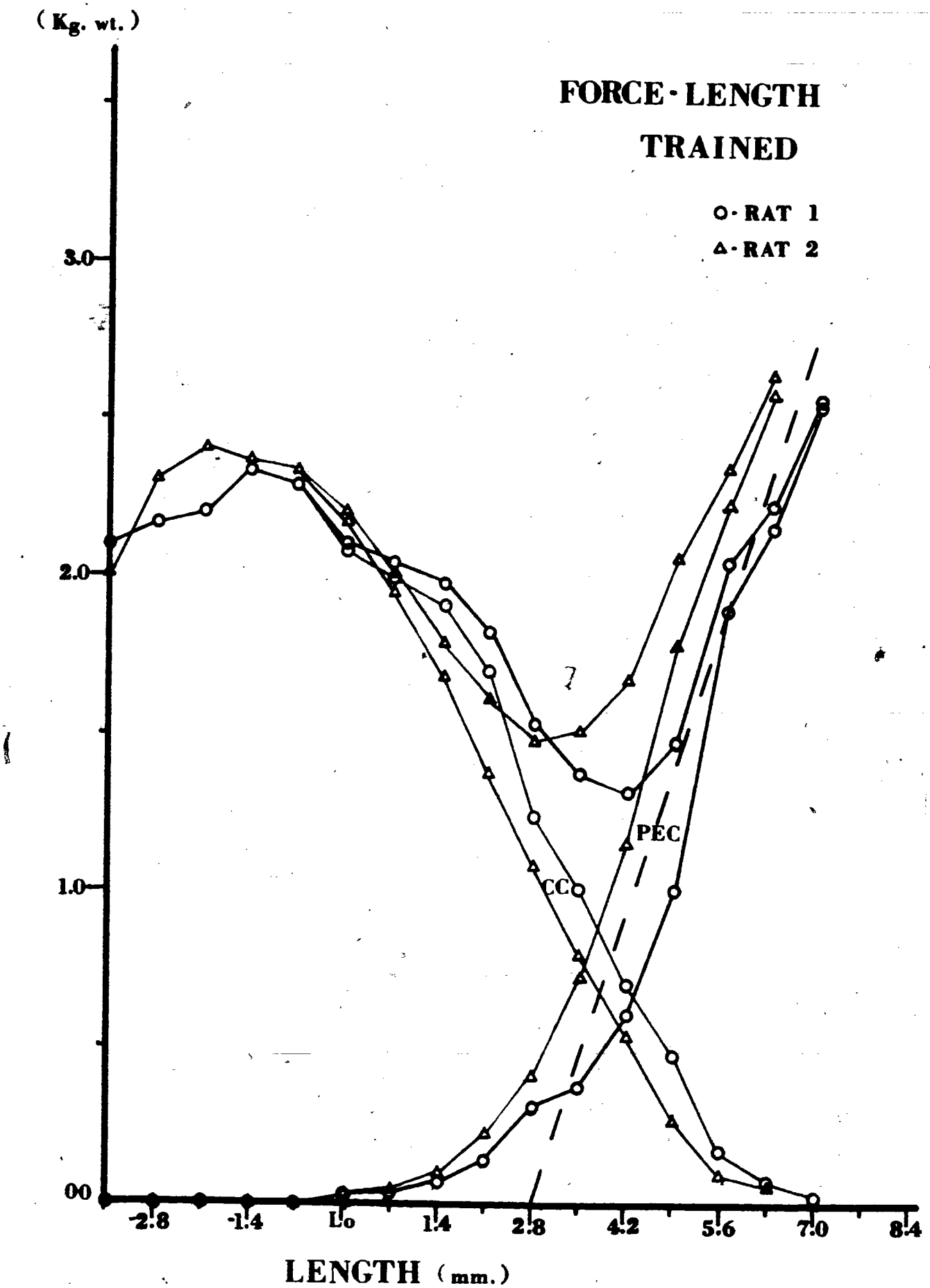
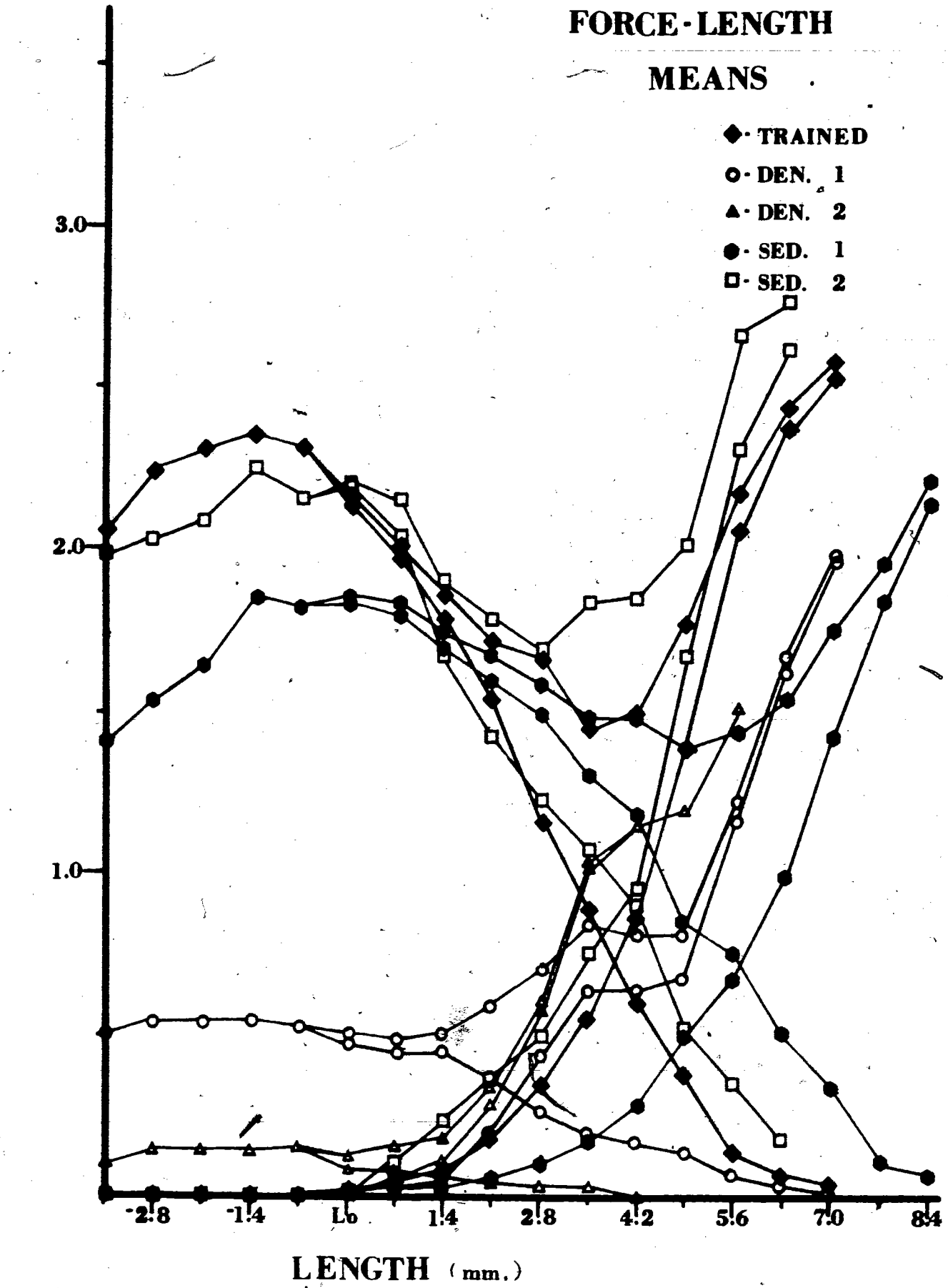

FORCE
(Kg. wt.)
FORCE · LENGTH
TRAINED
○ · RAT 1
△ · RAT 2
3.0
2.0
1.0
00
PEC
CC
-2.8
-1.4
Lo
1.4
2.8
4.2
5.6
7.0
8.4
LENGTH (mm.)

FIGURE 21:

Mean force-length relationships for rat groups presented in FIGURES 16 to 20. Mean force values were computed at equal increments of length.


FORCE
(Kg. wt.)
FORCE-LENGTH
MEANS
TRAINED
DEN. 1
DEN. 2
SED. 1
SED. 2
3.0
2.0
1.0
-2.8
-1.4
L6
1.4
2.8
4.2
5.6
7.0
8.4
LENGTH (mm.)

that of sedentary sub group 1. As observed in the previous section, denervation produced great reduction in isometric force, and this reduction persisted throughout a full change in length. It may also be seen in Figure 21 that the reduction in isometric force increased with the length of time after denervation. An examination of Figure 21 also revealed that the experimental treatments did not appear to affect the shape of the isometric F/L relationship of the CC.

ii) The Series Elastic Component

a). The Compliance-Force Relationship

The mechanical properties of the non-linear series elastic component (SEC) were examined in terms of changes in its compliance with respect to force (C/F relationship). In the linear analysis the SEC was equated with a purely elastic spring. Consequently only one value of compliance was obtained for all values of force. Both linear and non-linear C/F relationships for each of the various experimental treatments are shown graphically in Figures 22 to 27. Mean and standard deviations were computed for both linear and non-linear relationships of each group (Appendix 5). Graphic representation of the mean value curves for all the experimental groups were made in order to compare the linear values with the non-linear relationships (Figure 28). Mean and standard deviations for only the four major planned groups were plotted in order to give an indication of any significant differences between the groups which may have been due to the experimental treatments (Figure 29).

Statistical analysis was performed on the linear C/F relationship obtained from the denervated (sub-group 1), sedentary and trained (sub-group 2 groups. The data obtained from these groups was shown in TABLE 10

FIGURE 22:

The linear (straight lines) and non-linear compliance-force relationships for the SEC of rat gastrocnemius denervated one month.

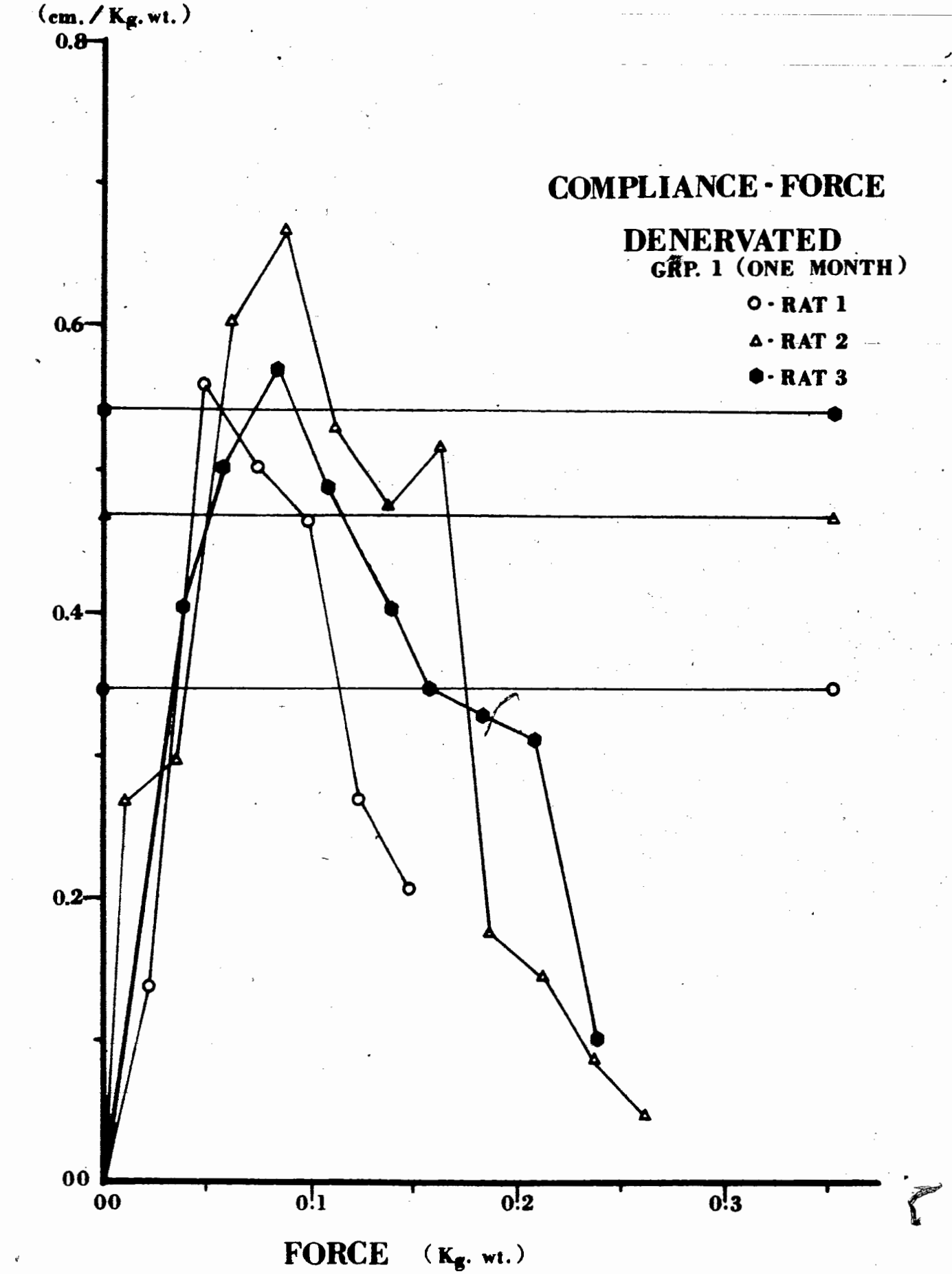

COMPLIANCE
(cm. / Kg. wt.)
0.8
0.6
0.4
0.2
00
00
0.1
0.2
0.3
FORCE (Kg. wt.)
COMPLIANCE - FORCE
DENERVATED
GRP. 1 (ONE MONTH)
○ - RAT 1
△ - RAT 2
⬢ - RAT 3

FIGURE 23:

The linear (straight lines) and non-linear compliance-force relationships for the SEC of rat gastrocnemius denervated two months.

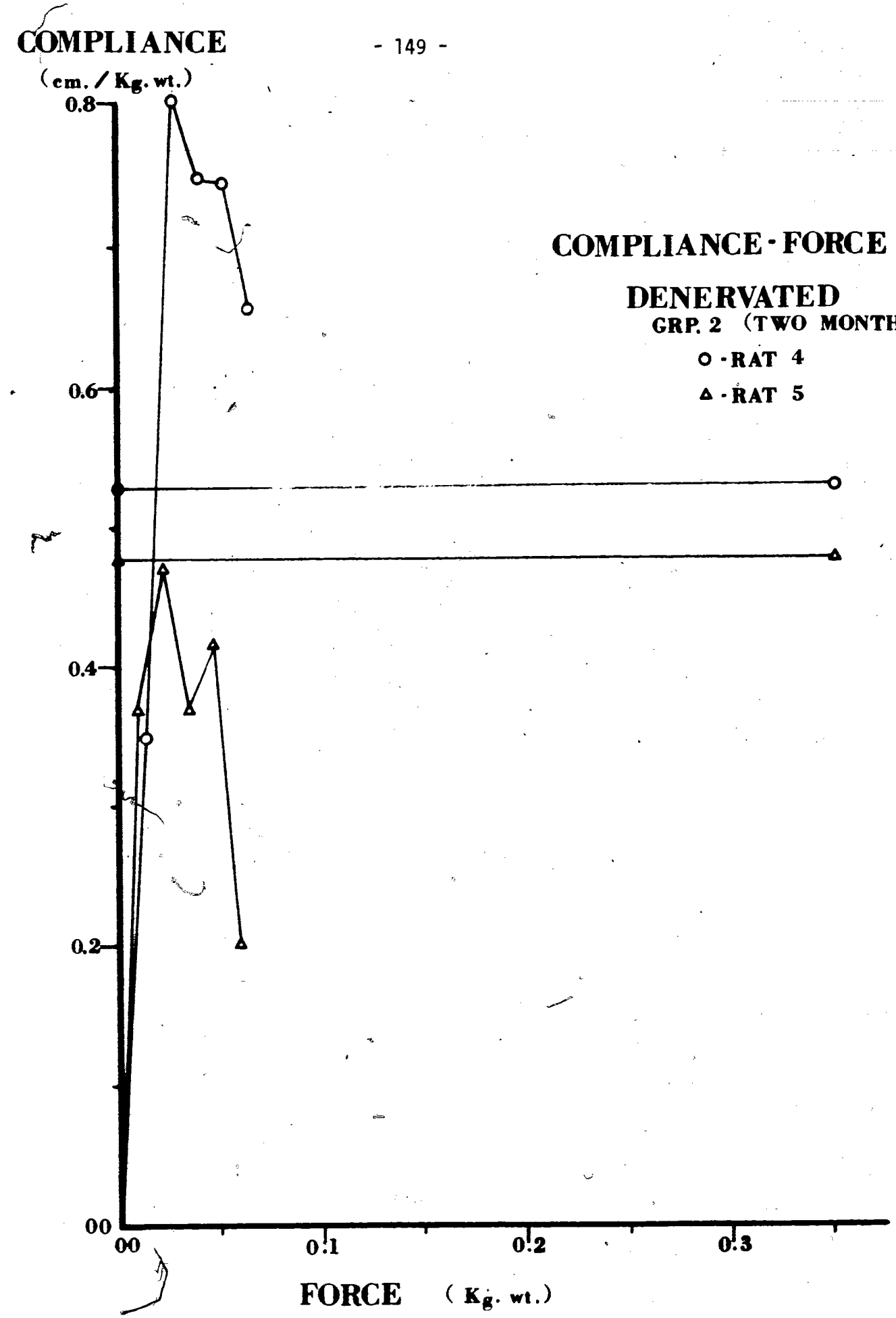

COMPLIANCE
(cm. / Kg. wt.)
0.8
0.6
0.4
0.2
00
00
0.1
0.2
0.3
FORCE (Kg. wt.)
COMPLIANCE - FORCE
DENERVATED
GRP. 2 (TWO MONTHS)
O - RAT 4
Δ - RAT 5

FIGURE 24:

The linear (straight line) and non-linear compliance-force relationships for the SEC of rat gastrocnemius when the anterior muscles were denervated one month.

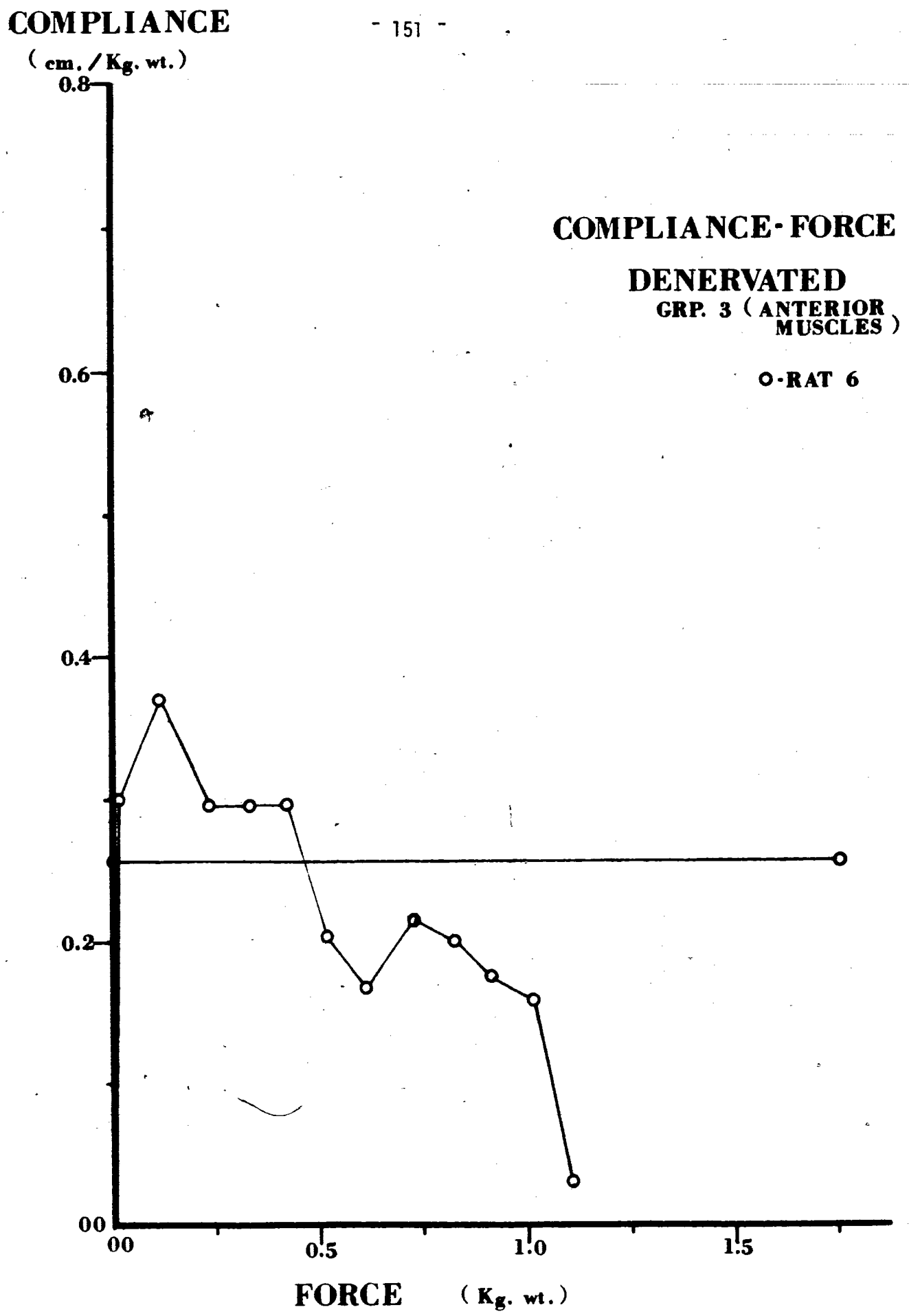

COMPLIANCE
(cm. / Kg. wt.)
0.8
0.6
0.4
0.2
00
00
0.5
1.0
1.5
FORCE (Kg. wt.)
COMPLIANCE - FORCE
DENERVATED
GRP. 3 (ANTERIOR MUSCLES)
O - RAT 6

FIGURE 25:

The linear (straight lines) and non-linear compliance-force relationships for the SEC of sedentary rat gastrocnemius.

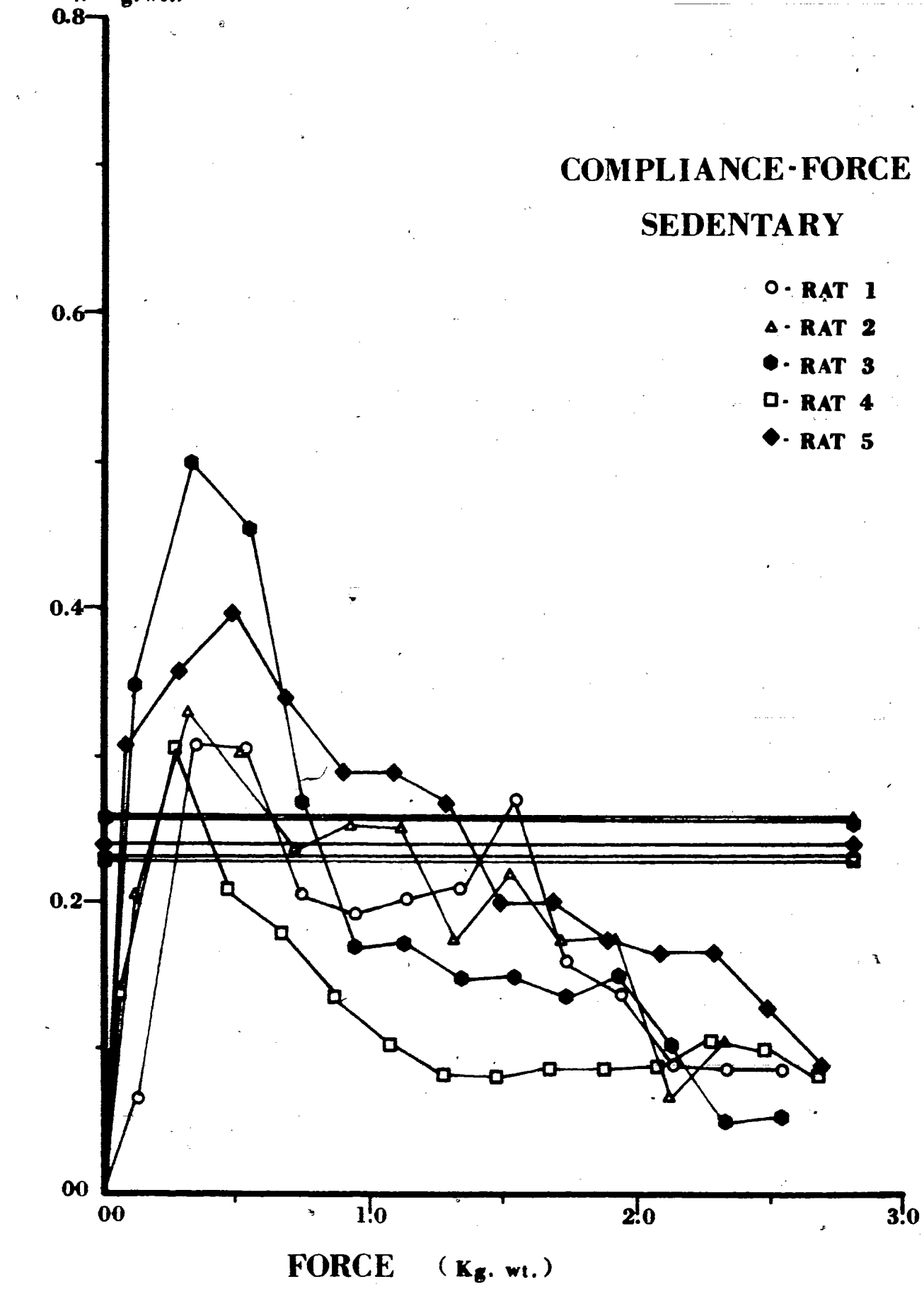

COMPLIANCE
(cm./Kg.wt.)
0.8
0.6
0.4
0.2
00
00
1.0
2.0
3.0
FORCE (Kg. wt.)
COMPLIANCE-FORCE
SEDENTARY
RAT 1
RAT 2
RAT 3
RAT 4
RAT 5

FIGURE 26:

The linear (straight lines) and non-linear compliance-force relationships for the SEC of trained rat gastrocnemius when the animal was sick.

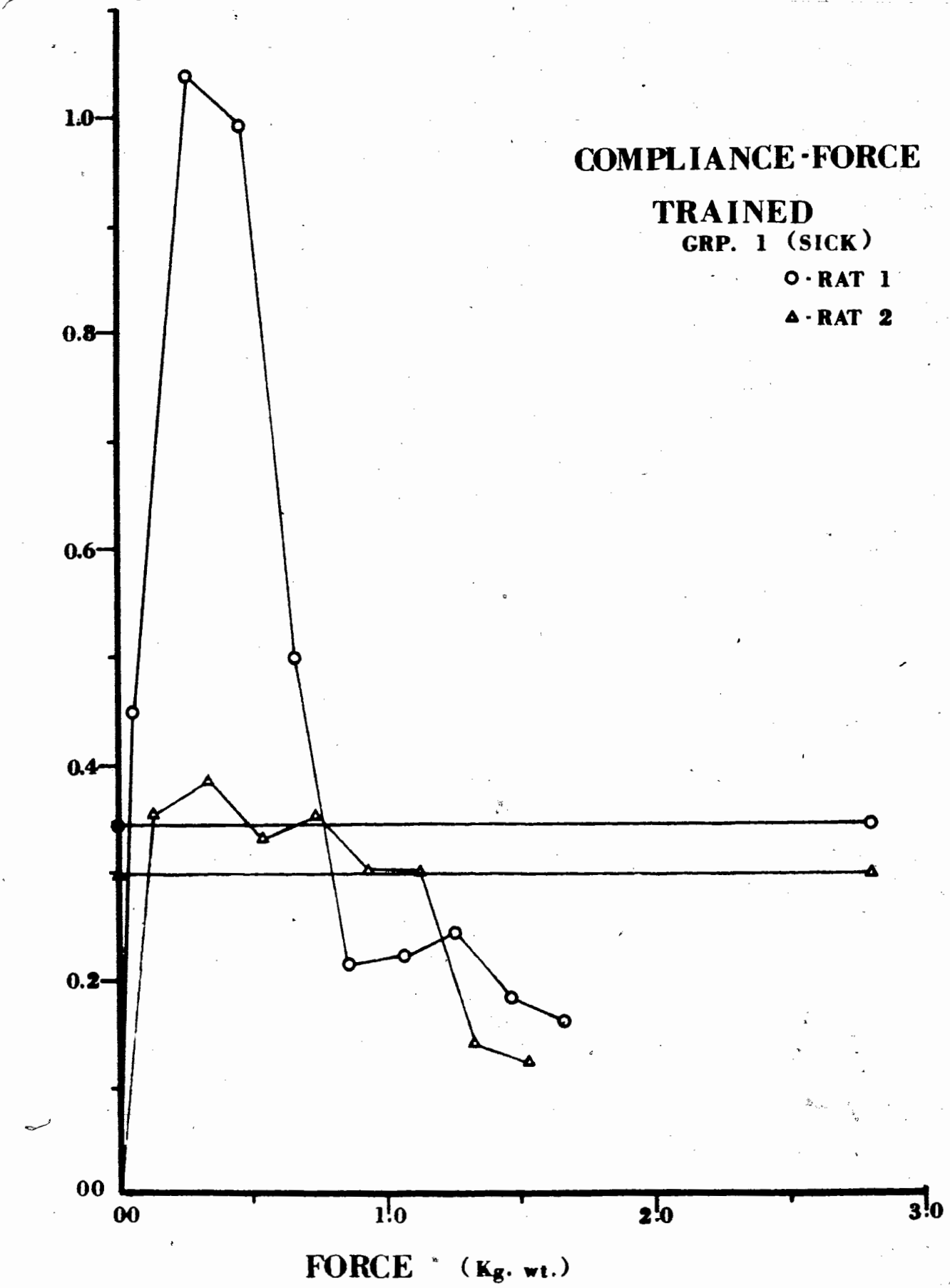

COMPLIANCE
(cm./Kg.wt.)
1.0
0.8
0.6
0.4
0.2
00
00
1.0
2.0
3.0
FORCE (Kg. wt.)
COMPLIANCE-FORCE
TRAINED
GRP. 1 (SICK)
O-RAT 1
Δ-RAT 2

FIGURE 27:

The linear (straight lines) and non-linear compliance-force relationship for the SEC of trained rat gastrocnemius.

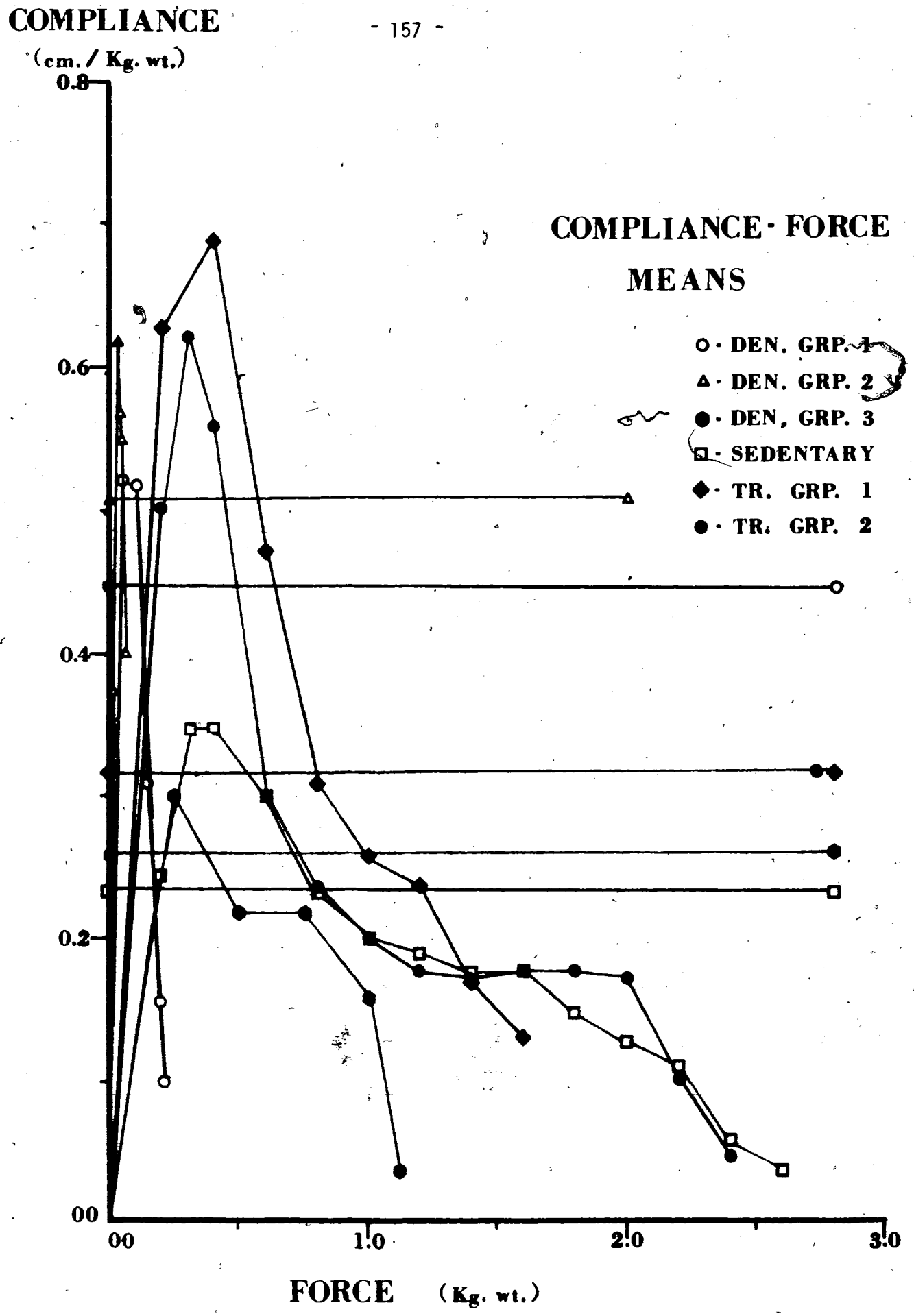

COMPLIANCE
(cm. / Kg. wt.)
0.8
0.6
0.4
0.2
00
COMPLIANCE - FORCE
MEANS
○ - DEN. GRP. 1
△ - DEN. GRP. 2
● - DEN, GRP. 3
□ - SEDENTARY
◆ - TR. GRP. 1
● - TR. GRP. 2
00
1.0
2.0
3.0
FORCE (Kg. wt.)

FIGURE 28:

The linear (straight lines) and non-linear compliance-force relationships for the SEC of rat groups presented in FIGURES 22 to 27. Mean compliance values were computed at equal increments of force for each group.

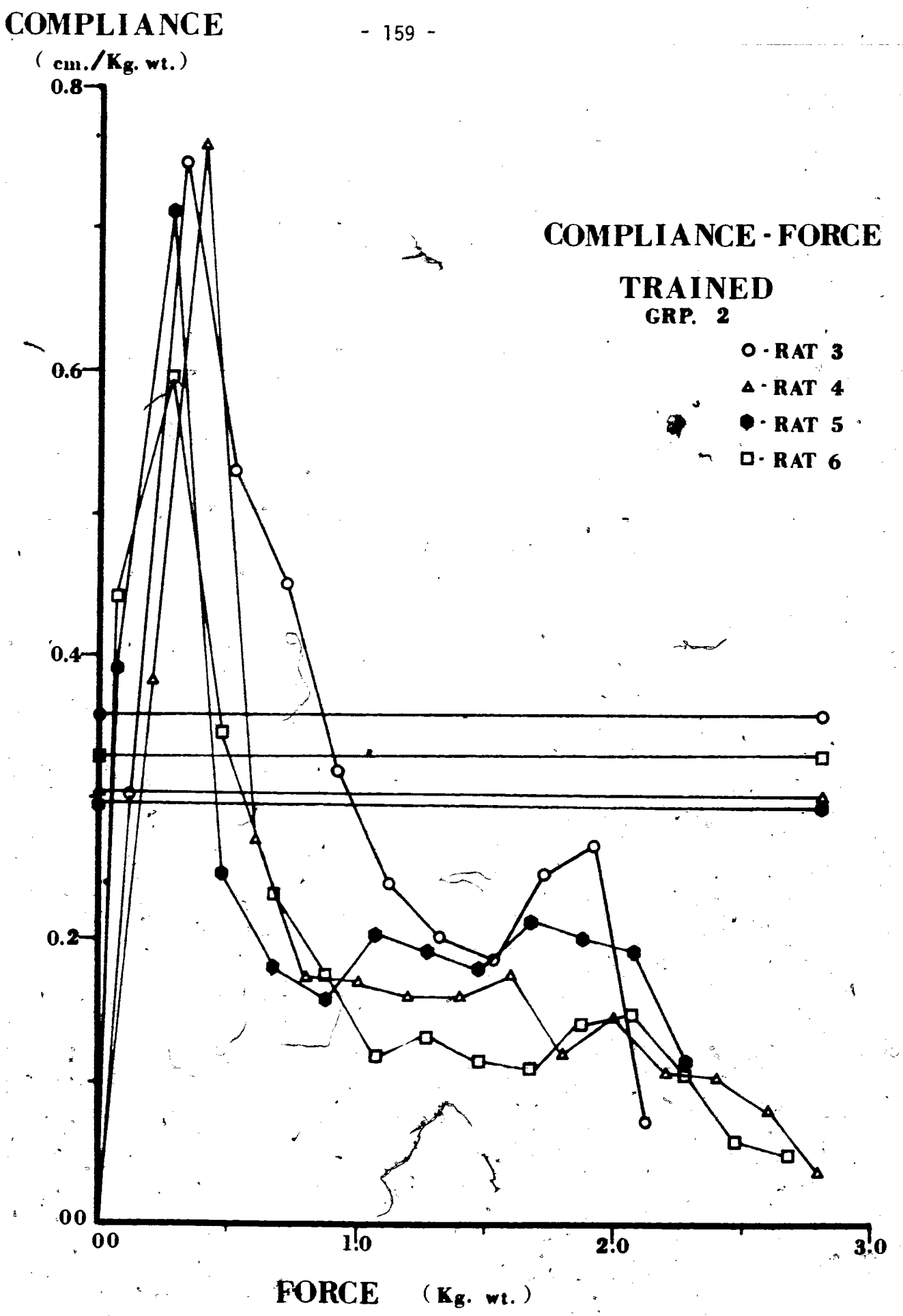
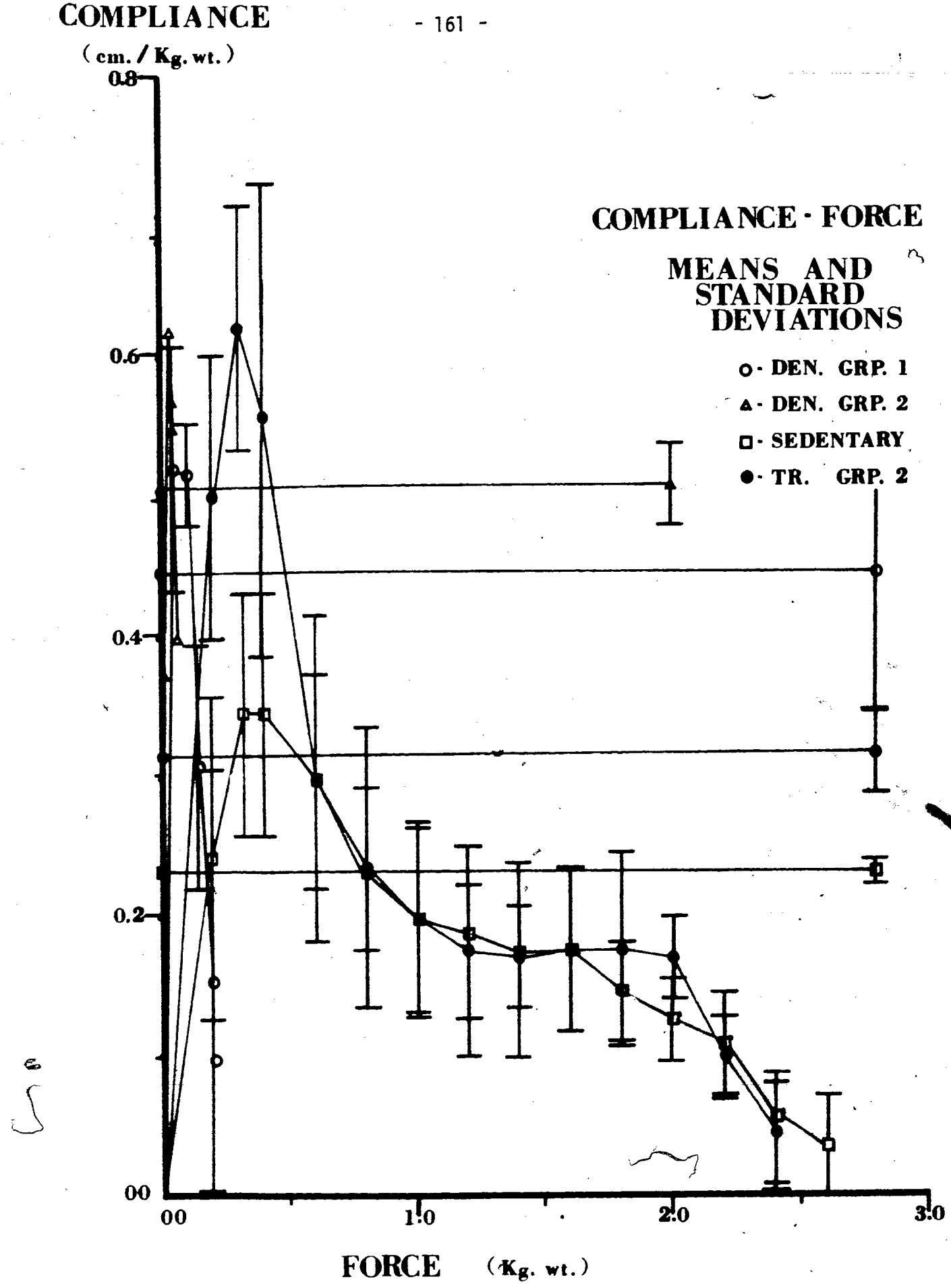

COMPLIANCE
(cm./Kg. wt.)
0.8
0.6
0.4
0.2
00
00
1.0
2.0
3.0
FORCE (Kg. wt.)
COMPLIANCE - FORCE
TRAINED
GRP. 2
O - RAT 3
△ - RAT 4
● - RAT 5
□ - RAT 6

FIGURE 29:

The linear (straight lines) and non-linear mean and standard deviation compliance-force curves for the SEC of the primary experimental groups.


COMPLIANCE
(cm. / Kg. wt.)
0.8
0.6
0.4
0.2
00
COMPLIANCE - FORCE
MEANS AND STANDARD DEVIATIONS
○ - DEN. GRP. 1
△ - DEN. GRP. 2
□ - SEDENTARY
● - TR. GRP. 2
00
1.0
2.0
3.0
FORCE (Kg. wt.)

and Appendices 4 and 5, while the application of the ANOV to this data was shown in Appendix 9. The use of the statistical analysis was justified by the fact that the linear C/F relationship was described by a single value ($C = \frac{1}{K}$, see TABLE 10).

The results of the ANOV was an F value of 16.08 which indicated significant differences among the mean compliances of the SEC obtained from each group. The mean compliance of the trained group was significantly greater than that of the sedentary group at an α-level of 0.01; and the mean compliance of the denervated group was also significantly greater (α-level of 0.01) than that of either the sedentary or trained groups (TABLE 14).

In an attempt to assess the effects of denervation and training on the linear and non-linear C/F relationships of the SEC, the changes obtained from statistical analysis of the linear C/F relationships required compariosn with the graphic representations of the non-linear C/F relationships (Figure 29). A significant difference was observed between the linear compliances of the sedentary and trained groups while the equivalent non-linear C/F curves in Figure 29 were not in accord with this finding. These curves were found to be almost coincidental of the greater part of their range except at low forces where the greatest difference between mean compliances was to be found. The large variance of data from both groups, except at 0.4 Kg force, negated the significance of any difference. It should be noted that the curves described were of the same shape. Alternatively, the mean linear compliances of the SEC of each group of denervated rats were far greater than those of the trained and sedentary groups. This finding was reflected in the non-linear C/F curves of the denervated groups shown in Figure 29. In this case the greatest compliance

was obtained at a much smaller force than the greatest compliance of either the sedentary or trained groups. While it should be noted that the greatest compliances of the denervated groups were comparable in magnitude with that of the trained groups, the subsequent drop in compliance with increasing force was far less than that obtained for either the sedentary or trained groups. In fact, there was less of a drop in compliance as the length of time after denervation increased. This observation can be verified by comparing the results obtained from denervated sub-group 1 with denervated sub-group 2.

b) The Extension-Force Relationships

An alternative way of observing the properties of the SEC is by examining the relationship between extension and force (E/F). Such a relationship was obtained from the C/F relationship by integrating compliance with respect to force. The linear equivalent of the non-linear E/F relationship was a line which had a gradient equal to the single linear value of compliance. The process of integration has been applied to the C/F curves shown in Figure 29 and the resulting linear and non-linear E/F curves are shown in Figure 30. The standard deviations shown were calculated from the same relationships using the maximum positive and negative deviations of compliance for each increment of force (Appendix 7).

Comparison of the linear and non-linear E/F relationships indicated a better agreement between the two systems of analysis than did the C/F relationship. The non-linear E/F relationship of the sedentary and trained groups were extremely similar in shape, while no significant difference could be suggested between these groups because of the magnitude of standard deviation. Yet a significant difference between the same sedentary and trained groups may be observed by consulting the linear

TABLE 14:

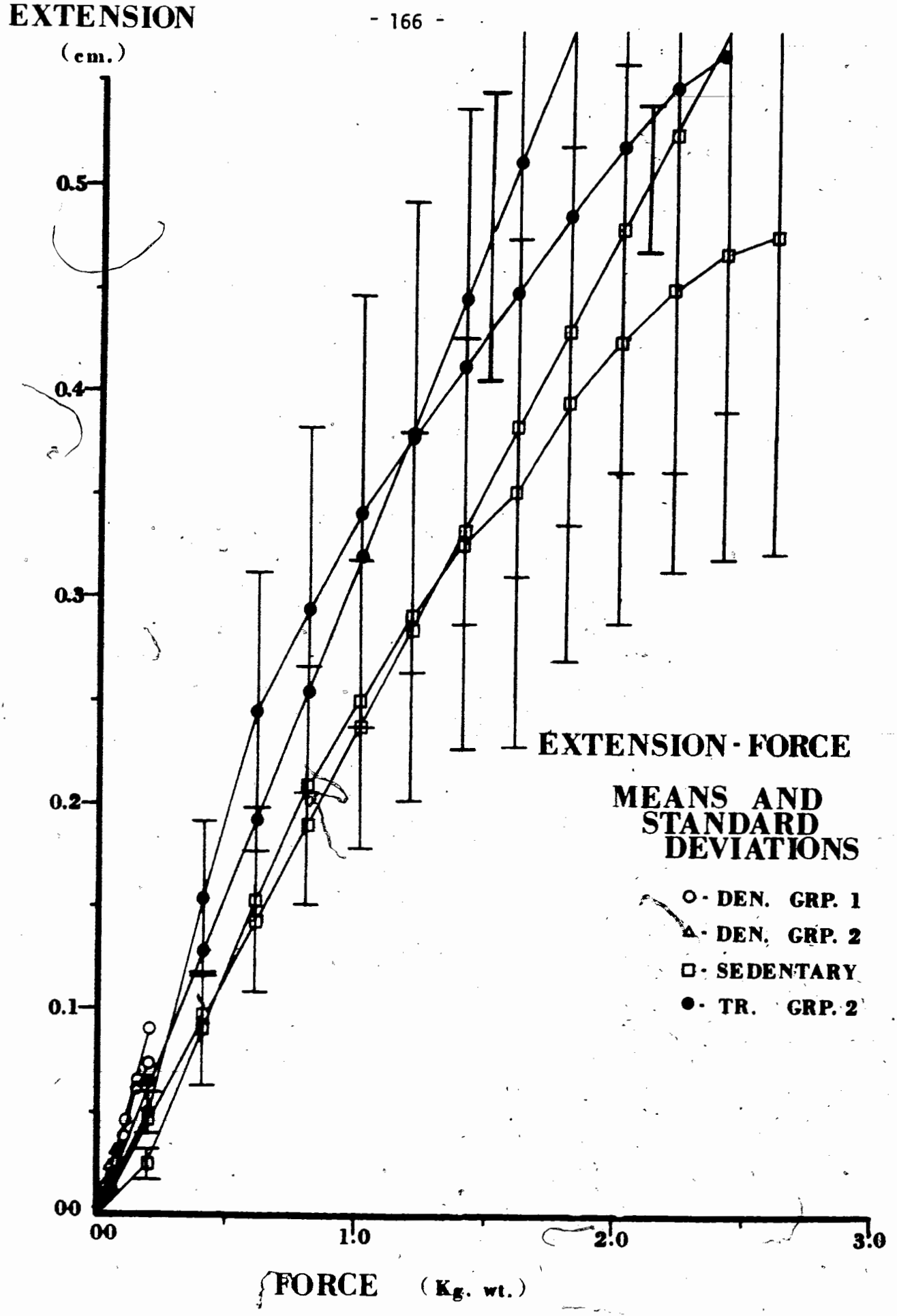
MEAN DIFFERENCES FOR C

GROUP	DENERVATED (1 month) 0.000454 cm./gm.wt.	SEDENTARY 0.000244 cm./gm.wt.	TRAINED (group 2) 0.000324 cm./gm.wt.
DENERVATED (1 month) 0.000454 cm./gm./wt.	---	0.000210**	0.000130**
SEDENTARY 0.000244 cm./gm.wt.	---	---	0.000080**
TRAINED (group 2) 0.000324 cm./gm.wt.	---	---	---

** Significant at an α-level of 0.01 (see Appendix 9)

FIGURE 30:

Results obtained by the application of the process of integration to FIGURE 29 produced the extension-force relationships for the primary experimental groups.


EXTENSION
(cm.)
0.5
0.4
0.3
0.2
0.1
00
00
1.0
2.0
3.0
FORCE (Kg. wt.)
EXTENSION - FORCE
MEANS AND STANDARD DEVIATIONS
DEN. GRP. 1
DEN. GRP. 2
SEDENTARY
TR. GRP. 2

values for both the C/F and E/F relationships.

iii) The Parallel Elastic Component

The effects of denervation, prolonged disuse and training on the mechanical properties of the parallel elastic component (PEC) can be assessed by examining the graphs obtained from the isometric F/L experiment (Figures 16 to 20). In general the non-linear behavior of the PEC was characterized by a decreased compliance (increased stiffness or gradient of the F/L relationship) with increased force. Figures 16 and 17 appeared to demonstrate a deviation from a smooth and regular decrease in compliance with increased force. This phenomenon appeared not only in both denervated groups but also in the same range of length of the muscle (between 3.5 mm. and 4.9 mm.). The latter fact suggested that the measurement of length by the displacement transducer was subjected to some error within a given range of lengths. Therefore the discontinuity in the change of compliance can not be attributed to the changes brought about by denervation. Inspection of Figure 21 revealed that in the lower range of increasing force the compliances of the denervated PEC's decreased more rapidly than those of the sedentary and trained groups. In the upper range of force the compliance was approximately constant and can be considered to represent the linear range of properties of the PEC. The compliances represented by the reciprocal of the slopes of those relationships (the interrupted lines in Figures 16 to 20) are shown in TABLE 15 along with the length at which the slope crossed the length axis of the F/L graphs.

The interrelationship of the calculated estimates of PEC compliance of the experimental groups was closely related to the results of the C/F relationships of the SEC. It was observed that prolonged denervation progressively decreased the compliance of the PEC when compared to the

base line group (sedentary sub-group 1), while the trained groups exhibited a similar decline in compliance of the PEC but at a reduced level. These findings indicated that both denervation and training brought about stiffening of the PEC but that the effects of these experimental treatments were not as great as prolonged disuse (sedentary sub-groups 2, TABLE 15).

The decline in compliance of the PEC due to these experimental treatments was also reflected in a reduced length at which the tangent crossed the length axis of the F/L graphs (TABLE 15). The overall trend of these results was consistent with that demonstrated by compliance, where denervation and training both resulted in a reduced length axis intercept. Only when the trained and sedentary (sub-group 2) groups were compared were there any distinct differences in the trend. It should be noted that when these groups were compared it was observed that the trained group exhibited a much lower length at which the tangent crossed the length axis of the F/L graphs. The latter finding suggested that the compliance of the PEC demonstrated an earlier involvement in length changes of the muscle in the trained group that in any other group whether denervated or disused for extended periods of time.

iv) The Relationship Between Linear and Non-Linear Measurements of Mechanical Properties

In this thesis the mechanical behavior of the musculo-tendinous system has been examined in relation to models containing completely linear and non-linear elements. Although the properties of elements of this system are known to display non-linear behavior, linear estimates have been used by a number of authors because of the ease with which the linear model can be analyzed. The mathematical processes by which the correspondence between linear and non-linear models was determined has

TABLE 15:

ESTIMATED SLOPE OF THE PEC

GROUP	SLOPE OF TANGENT (Kg.wt./mm.)	COMPLIANCE OF THE PEC (cm./fm. wt.)	LENGTH INTERCEPT AXIS (mm.)
DENERVATED (1 month)	0.689	(.000145)	3.9
DENERVATED (2 months)	0.741	(.000135)	2.0
SEDENTARY (group 1)	0.571	(.000175)	4.5
SEDENTARY (group 2)	1.111	(.000090)	3.3
TRAINED	0.645	(.000155)	2.7

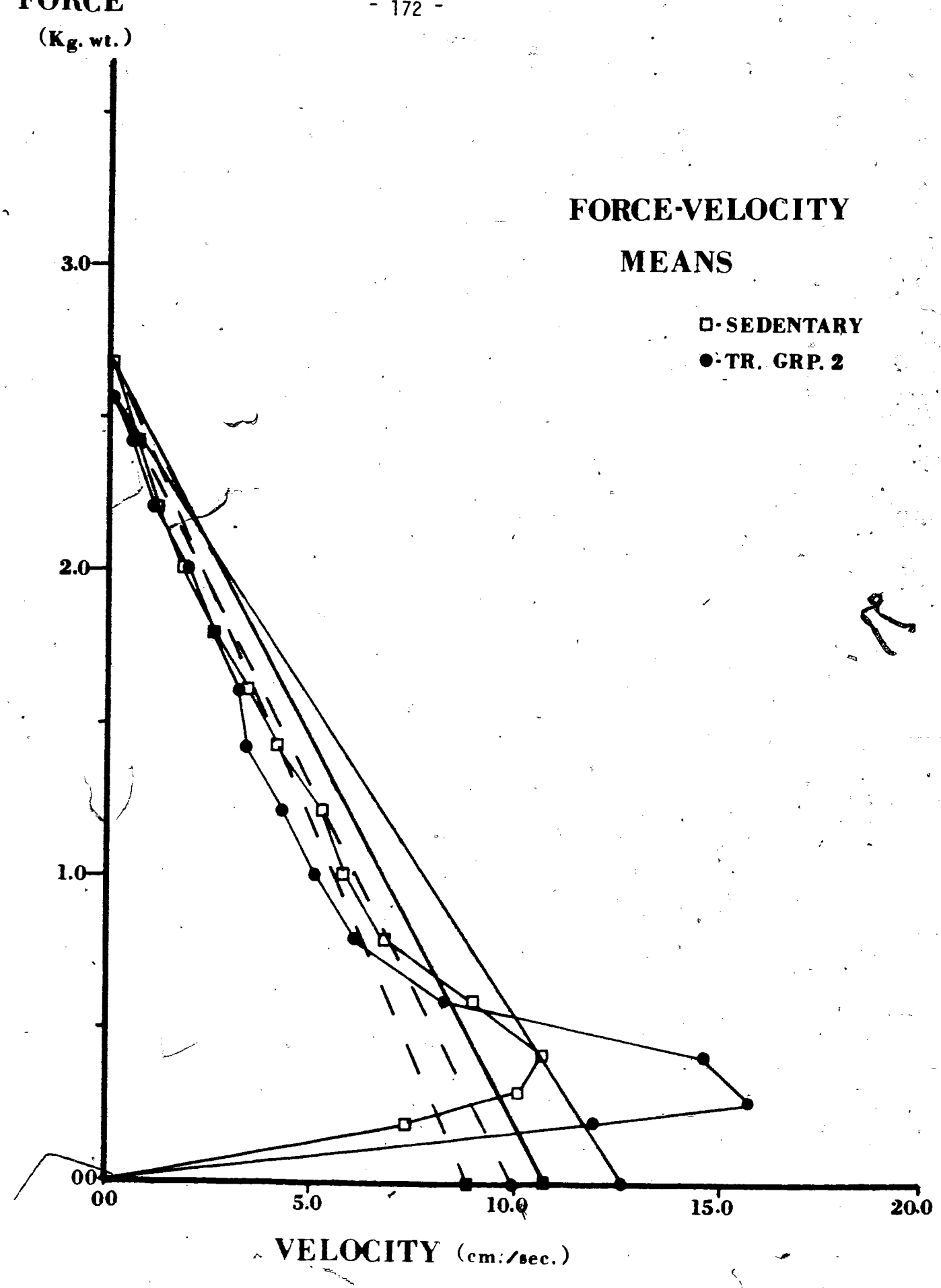
been shown in the section on Methods of Analysis (Chapter III). Figure 31 shows both linear and non-linear F/V relationships obtained from the sedentary and trained (sub-group 2) groups of rat muscles. The broken lines shown in this figure represent the linear relationship calculated as being mathematically equivalent to the non-linear relationship. As can be seen, the linear relationships obtained from the application of the linear analysis tended to produce a decreased slope of the linear F/V relationship with a consequent overestimate of the maximal velocities of shortening. Even with this overestimate of V_{max} the comparison between results obtained from the sedentary and trained groups was apparently the same when determined by either the linear analysis or the mathematical equivalent.

Linear C/F relationships for the same groups were calculated mathematically using the method previously mentioned. Similar results were found in that the linear C/F relationship obtained from the linear analysis represented an overestimation of the mathematically calculated linear compliance for both sedentary and trained groups (Figure 32). The general effect of training on the SEC indicated by the C/F relationship resulting from the linear analysis was still shown by the mathematical equivalent of the non-linear relationship.

Integration of the linear C/F relationships which were calculated from the non-linear C/F relationships produced the theoretical linear E/F relationships for both groups. The results indicate consistent overestimation of the gradient of the E/F relationship when the latter was obtained from the original linear models (Figure 33). Although the overestimates of the gradient of the E/F relationship for both groups corresponded in magnitude (≈20%) with those found for the F/V and C/F relationships, it should be mentioned that the mathematical equivalent linear E/F relationships did

FIGURE 31:

The non-linear and linear force-velocity relationships obtained experimentally for the sedentary and trained groups (solid lines) as shown in Figure 15. In addition the theoretical linear force-velocity relationships calculated from the non-linear relationships (broken lines). (See Text)


FORCE
(Kg. wt.)
FORCE-VELOCITY
MEANS
□-SEDENTARY
●-TR. GRP. 2
3.0
2.0
1.0
00
00
5.0
10.0
15.0
20.0
VELOCITY (cm./sec.)

not appear to produce a better fit for the non-linear E/F relationships fo either group.

At first these results were quite surprising but an explanation was found after examining the original assumption of the linear model. The model initially assumed that the force generator (Fm) was activated maximally and instantaneously. This assumption held true for dynamic contractions where the muscle would be totally activated at the time measurement would be taken. On the other hand, the analysis of isometric contractions involved the total development of force from an inactivated to a totally activated state. Therefore, the isometric myogram showed a slow rise in force just after the onset of stimulation which then rose quicly before gradually slowing as P_o was approached. The accomodation of the original assumption of the linear model required that the early rise in force had to be negated to produce the desired exponential force-time curve or isometric myogram (Figure 34). Therefore the time taken to reach 63.2% of P_o would have been calculated as being less than the real time taken to reach 63.2% of P_o. It was observed that the under-estimates of the time (τ) to 63.2% was approximately equal to the 20% overestimation reflected by the linear relationships presented for the mechanical behavior of the CC and SEC.

FIGURE 32:

The non-linear and linear compliance-force relationships obtained experimentally for the sedentary and trained groups (solid lines) as shown in Figure 29. In addition, the theoretical linear compliance-force relationsips calculated from the non-linear relationships (broken-lines). (See Text).

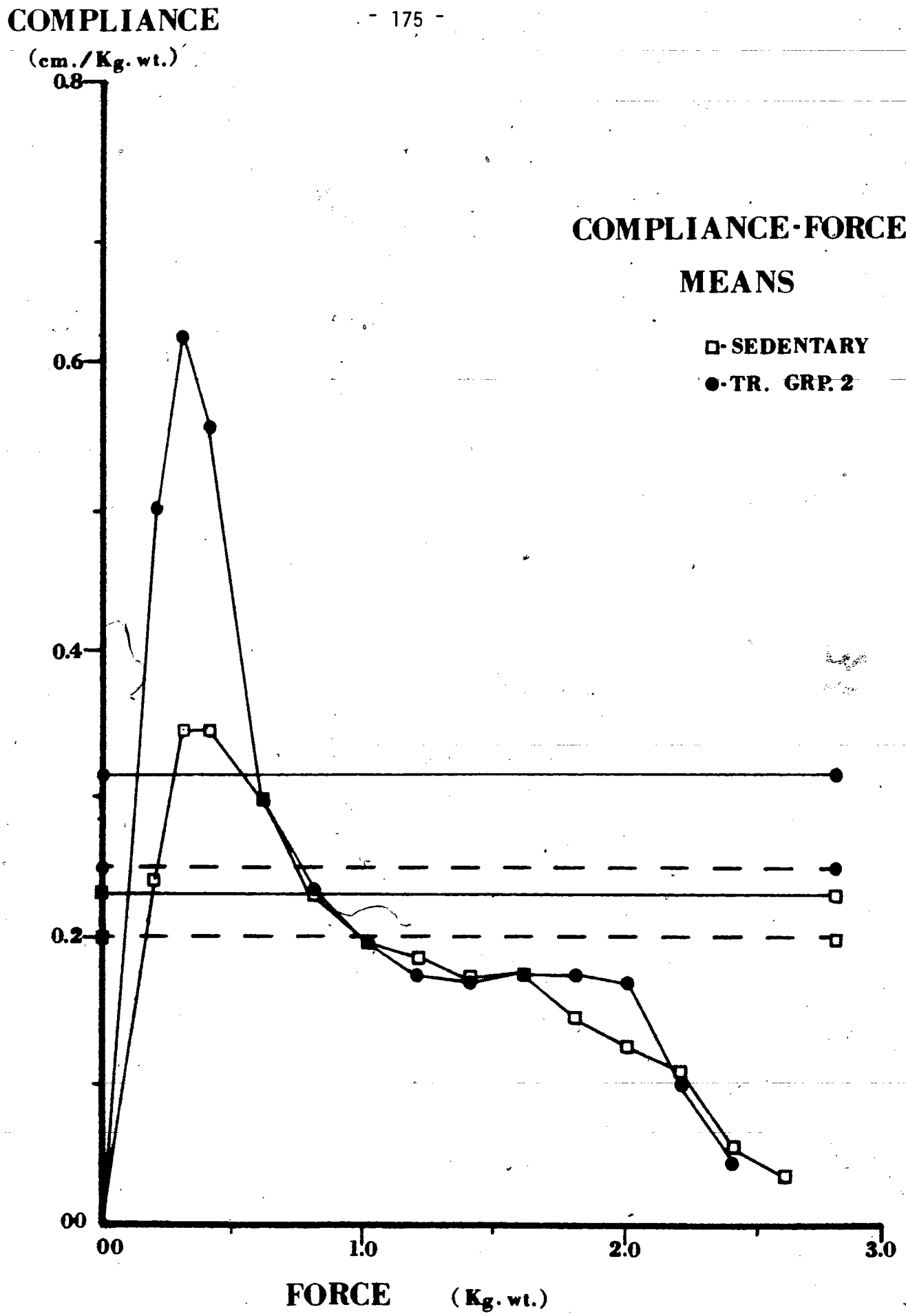

COMPLIANCE
(cm./Kg. wt.)
0.8
0.6
0.4
0.2
00
00
1.0
2.0
3.0
FORCE (Kg. wt.)
COMPLIANCE-FORCE
MEANS
SEDENTARY
TR. GRP. 2

FIGURE 33:

The non-linear and linear extension-force relationships obtained experimentally for the sedentary and trained groups (solid lines) as shown in Figure 32. In addition, the theoretical linear extension-force relationships calculated from the non-linear relationships (broken lines). (See Text).

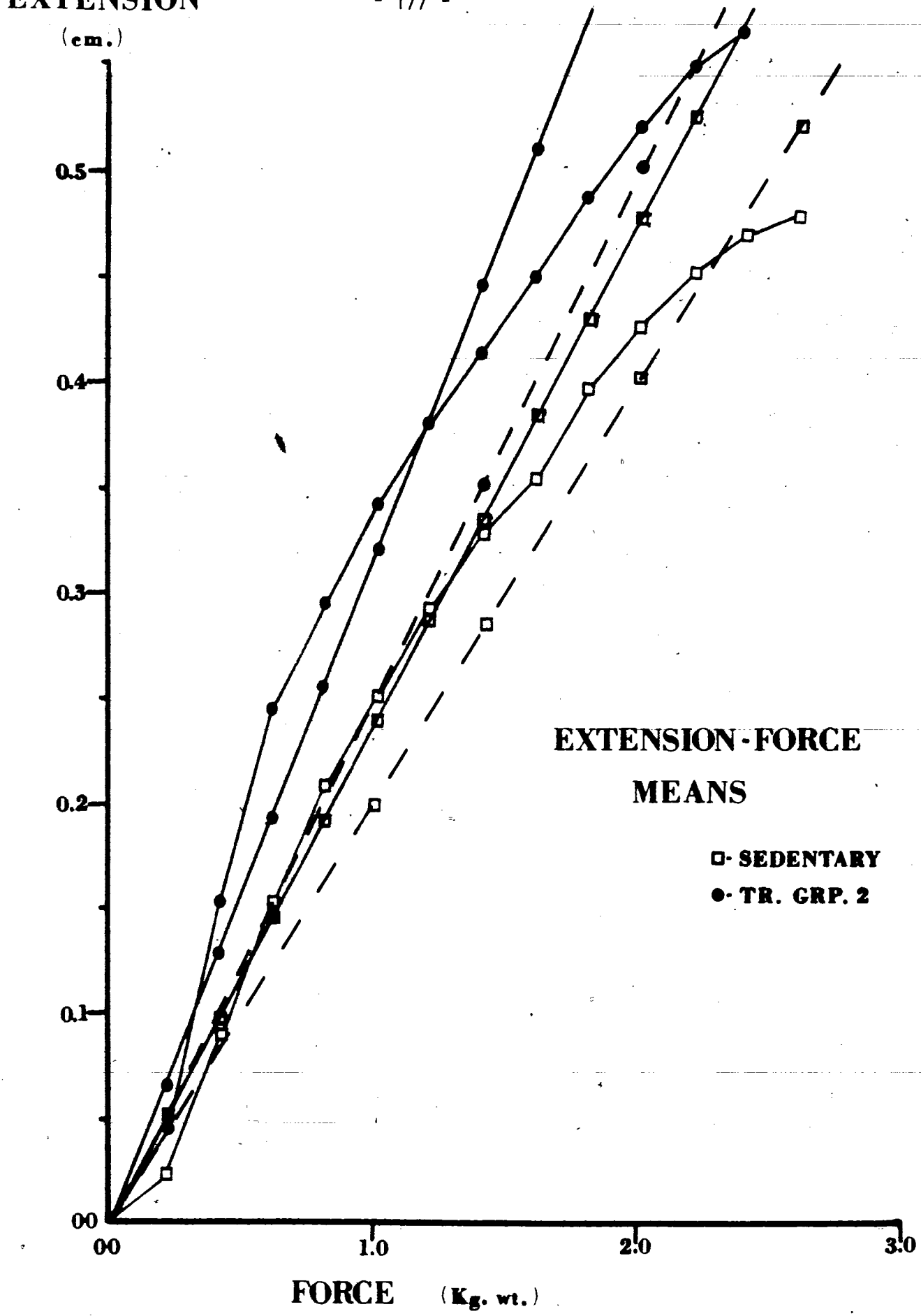
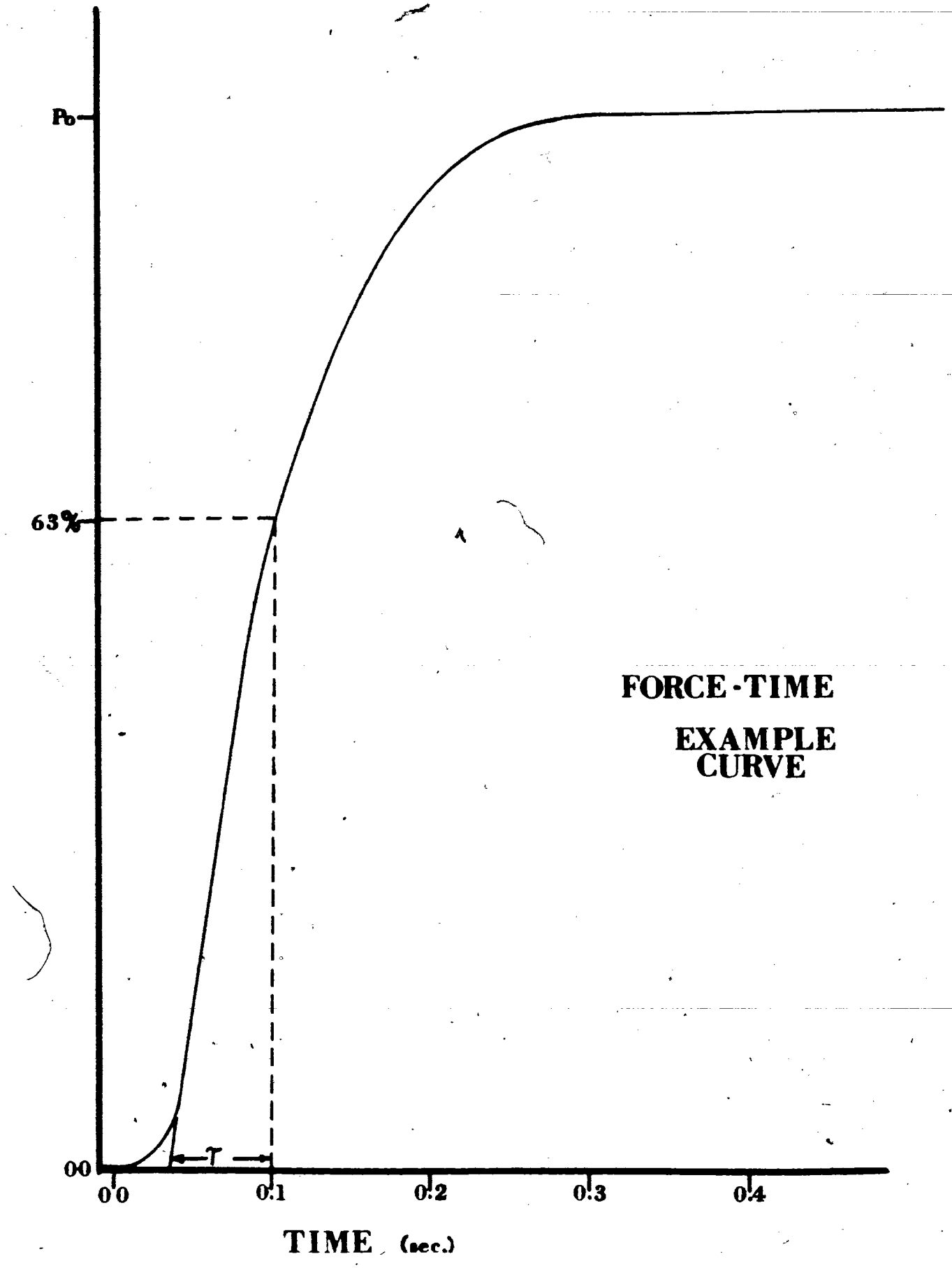

EXTENSION
(cm.)
0.5
0.4
0.3
0.2
0.1
00
00
1.0
2.0
3.0
FORCE (Kg. wt.)
EXTENSION - FORCE
MEANS
□- SEDENTARY
●- TR. GRP. 2

FIGURE 34:

Graphic representation of a force-time (isometric myogram) curve resulting from an isometric contraction. Indicates a possible explanation for overestimations presented by linear analysis.


FORCE
Po
63%
00
T
0·0
0·1
0·2
0·3
0·4
TIME (sec.)
FORCE-TIME
EXAMPLE
CURVE

CHAPTER V

DISCUSSION

A. ANATOMICAL EFFECTS OF DENERVATION AND TRAINING

The various treatments did not affect BW in any significant way although some changes in percentages of muscle and fat may have been the result of the different levels of activity of the groups. However, such changes may have been cancelled out leaving no overall changes in BW.

As both the denervated and sedentary groups were confined in cages, the only possibility which may have led to differences in BW was the atrophy of the denervated muscle. As the weight of a single gastrocnemius muscle amounted to approximately 0.4% of the total BW, the similar eventual BW's of the two groups were to be expected. An epidemic of pneumonia resulted in the deaths of a number of rats, but this factor was common to all experimental groups. Thus it is concluded that denervation should have little or no effect on BW because postoperative situations were identical for all groups and, that severing the tibial nerve affected only a small percentage of the total BW.

Theoretically, changes in mean BW brought about by a specific training program could be used as an indicator of the progress of that program if the results of Mayer (1960) are used as a guide line. The major problem with using changes in BW as an indicator of the effects of training is that the term "optimal exercise" is ambiguous and somewhat arbitrary. Mayer (1960) indicated that rats trained at below optimal or optimal levels of exercise would demonstrate significant increase in BW while overactivity would result in reduced BW measurements. Although there was a small increase in mean BW of the trained group of 20.9 gm.wt. (≈3.3%

total BW), this increase was not significant when compared with the mean BW of the sedentary groups. Further investigation showed that the differences between the results of the present study and those of other authors were probably due to the different training program used. Therefore, the results of denervation and training cannot be realistically measured in terms of BW. Consequently, a more precise indication of the effects of a localized treatment can be obtained by examing the structure of the muscles. Thus the effects of denervation and training can best be assessed by comparing the mean MW and ML of the gastrocnemius of these groups with those of the disused muscles.

Statistical analysis of the mean MW's for the denervated (sub-groups 1 and 2), sedentary and trained groups indicated that there were significant differences between each pair of the four groups at the α-level of 0.01 (TABLE 7). These findings showed that the denervated groups demonstrated a progressive loss in mean MW when compared to the mean MW of the sedentary groups.

The observed decreases in mean MW presented by the denervated groups were in close agreement with the observations of other authors. It was found that the loss in mean MW of the denervated rat gastrocnemius was 40.2% (1.9948 gm.wt.) at the end of one month and 54.7% (2.7131 gm.wt.) after two months. Through histochemical analysis it was shown that all fibre types present in rat gastrocnemius were reduced in cross-sectional area by at least 80% after two months of denervation. These observations substantiate those of Sunderland and Ray (1950), Pellegrino and Franzini (1963) and Miledi and Slater (1969). Subsequently, it was concluded that the progressive loss in MW over two months of denervation was the direct result of atrophy of the composite muscle fibres in the denervated rat

gastrocnemius.

TABLE 7 indicates that training produced a significant difference between mean MW;s of the trained and sedentary groups at an α-level of 0.01. The mean difference of 0.5277 gm.wt. represented an increase in mean MW of 10.6% over that of the sedentary groups. Both Gordon et.al. (1967) and Barnard et.al. (1970, Part II) showed that there was a decrease in mean MW for animals trained by low intensity running. Obviously the results of the present study do not correspond with the findings of these authors. Such disagreeing results of anatomical measurements of trained animals suggest further support for the earlier conclusion that the training programs used by Gordon et.al. (1967) and Barnard et.al. (1970, Part II) cannot be compared with that used in the present investigation. However, some interesting statements can still be made when considering the findings of these and other investigators.

Gordon et al. (1967) suggested that repetitive exercises enhance the concentration of energy liberating enzymes (sarcoplasmic proteins) resulting in the development of local muscle endurance while forceful exercise developed increased strength through increases in the concentration of myofibrillar proteins. Similar results for low intensity running were presented by Holmes and Rasch (1958) and Barnard et.al. (1970, Part II); while the findings of Helander (1961) demonstrated that increases in myofibrillar proteins may be indicated by an increase in MW. The results of the present investigation suggest an increase in muscle volume and a significant increase in mean MW during training which would suggest increases in both sarcoplasmic and myofibrillar protein concentrations.

The inconsistancies of MW results between the present study and those of other authors may indicate that increases or decreases in sarco-

plasmic and myofibrillar protein concentrations can be used as an index to distinguish the various types of training procedures and that MW trends are subject to question. Without biochemical analysis, the only method of determining which factor (ie., sarcoplasmic or myofibrillar protein concentrations) resulted in the observed increase in mean MW was to examine the mechanical behavior of the trained muscles. Holmes and Rasch (1958), Gordon et.al. (1967) and Barnard et.al. (1967) suggested that myofibrillar protein concentrations can be used as an indicator of force of contraction of muscle. The present study shows a significant increase in the maximal velocity of shortening (V_{max}) with no change in the maximal force (P_o) of contraction of the trained compared with sedentary muscles (TABLES 12 and 13). Therefore, it is concluded that the observed increase in mean MW of the trained group was the result of increased sarcoplasmic protein concentrations and may be indicative a faster release of calcium into the muscle sarcomeres.

Very little work has been performed to determine the effects of denervation and/or training on ML because this measurement has been assumed to provide relatively little information. TABLE 8 indicated that there were significant differences in mean ML between each of the denervated and the sedentary groups. This same table indicated that there was no significant difference between the two denervated groups, or between the sedentary and trained groups.

It was found that there was a 3.7 mm. increase in mean ML after one month of denervation. This increase represented a figure more than 50% larger than that obtained by Stolov and Weilepp (1970). It is suggested that the 3.7 mm. increase in mean ML may not be indicative of the actual effects of denervation over a one month period due to the large

differences in the individual ML measurements (TABLE 6). Obviously larger experimental groups were necessary to produce an accurate assessment of the effects of denervation over this period.

The variability in results observed for the individual ML's of rat gastrocnemius denervated for one month might suggest that the effects of denervation over this period are quite dramatic and individually oriented. Pellegrino and Franzini (1963) indicated that the earlier stages of the degenerative processes involved in denervation fluctuated while stabilizing after a one month period of denervation. The findings of these authors and of Miledi and Slater (1969) indicate that the most dramatic changes in muscle due to denervation atrophy were observed after one month of denervation; and that after one month these changes stabilized, becoming less significant as time progressed. Stolov and Weilepp (1970) suggested that there was a direct relationship between atrophy of the individual muscle fibres and muscle elongation where the ML increased as atrophy of the fibres progressed.

The trends exhibited by the mean MW and ML of the denervated muscles suggests that this relationship does indeed exist where the most dramatic and fluctuating differences were observed in the first month of denervation. Therefore, it is concluded that the rat gastrocnemius, which is a pennate muscle, demonstrated a unique relationship between increased mean ML and mean MW during prolonged denervation.

Stolov and Weilepp (1970) made an additional suggestion that muscle elongation due to denervation may also be the result of the effects of an active group of antoagonistic muscles. This interplay between muscles was demonstrated by the ML measurements of all the denervated animals in the present study (TABLE 6). In one instance the anterior dorsi flexor

muscles were denervated resulting in permanent shortening of the antagonistic muscles (gastrocnemius and soleus) with consequent plantar flexion (denervated rat #6, TABLE 6). All the other denervated animals demonstrated permanent dorsi flexion due to denervation of the gastrocneius and soleus muscles. Therefore, denervation of any group of muscles would result in limited control over the activities of the antagonist muscles and therefore produce active elongation of the denervated muscles.

Isolated denervation of the plantar flexors (gastrocnemius and soleus muscles causes elongation of those muscles and shortening of the antagonist muscles. Furthermore, it was suggested that there was a direct relationship between atrophy and elongation of denervated muscle. It seems likely that both processes were involved in muscle elongation, but to what extent their involvement accounted for changes in ML is unknown. It is isggested that the involvement of each of these factors could be assessed by the use of two denervated groups of animals, the first of which would have the plantar flexors denervated while the latter group would have both the plantar and dorsi flexors denervated. By employing the results of these two groups an accurate assessment of the effects of the antagonisti muscles on the elongation of the plantar flexors could be obtained during denervation.

The effects of training on mean ML were found to be insignificant (TABLE 8). Although there was a small decrease in mean ML no conclusions could be derived concerning changes in the mechanical behavior of the trained muscles.

B. EFFECTS OF DENERVATION ON MUSCLE STRUCTURE

The present study verified the existence of the three fibre types

in rat gastrocnemius by estimating the activity of succinate dehydrogenase. Although large amounts of histochemical and biochemical research has involved the use of a number of rat muscles, no reference could be located which described the muscle fibre composition (in terms of % total) of rat gastrocnemius.

The sedentary rat gastrocnemius had a fibre composition of 15.2% red, 55.9% white and 28.8% intermediate. It is observed that these values for fibre composition of rat gastrocnemius are within the ranges found for the three fibre types present in cat gastrocnemius (Close, 1972). Histochemical data colledted for rat and cat soleus muscle, which is a muscle closely related to the gastrocnemius, indicate that there were significant differences in fibre composition of about 20% between these animals (Close, 1972). Consequently, a comparison between rat and cat gastrocnemius is questionable in that the similarities demonstrated may have been only coincidental.

Denervation fo the rat gastrocnemius resulted in an observed decrease in white fibre composition (55.9% to 34%) which produced relative increases in the red (15.2% to 24%) and intermediate (28.8% to 42%) fibres. Marin and Denny-Brown (1965) noted similar results and indicated that there were increased numbers of red fibres as atrophy due to denervation progressed and that histochemical studies revealed a greater reduction in the number and size of the white muscle fibres. Thus it can be concluded that denervation atrophy of muscle was responsible for a reduced number of white muscle fibres which was partially indicated by a relative increase in red and intermediate fibre concentrations. Therefore the data demonstrated that there was no increase in the red and intermediate muscle fibre population and that the percent composition indicated only a

decrease in the white fibre numbers.

A close examination of PLATES 6 and 7 revealed that there was a significant decrease in the mitochondrial activity for all fibres in the denervated section as was indicated by the intensity or degree of staining. Hachmias and Padykula (1958) noted that in the rat, denervation produced a decrease in succinate dehydrogenase activity, a reduction in glycogen and lipid content while ATPase content was not affected. It was concluded by Romanul and Hogan (1965) that individual fibre types lost those enzymes normally present in higher concentrations, whereas there was little or no change in enzymes normally low. The enzymatic and thus the mechanical distinctions of the individual fibres evidently tend to be lost during prolonged denervation.

The lack of distinction between the three types of muscle fibres due to denervation was enhanced further by the estimates of fibre size. It was found for sedentary rat gastrocnemius that white muscle fibres (48.8 μ) were twice the size of red fibres (23.3 μ) with the intermediate fibre size (30.2 μ) being between the red and white fibre sizes. In contrast, the denervated tissue demonstrated reduction in size of all three fibre sizes. The most drastic decrease in size was recorded for the white muscle fibres of the denervated tissue, where the size of these fibres were found to be 66% smaller (16.2 μ) than the sedentary measurements of the same fibre. Reductions in the size of the red and intermediate muscle fibres were also found to be significant and were estimated to be 50% (11.6 μ) and 46% (13.9 μ) respectively (TABLE 9). These findings implied that progression of denervation resulted in a trend towards integration of the three muscle fibres.

Comparison of measurements of the denervated fibres with those

attained for the sedentary muscles indicated dramatic reductions in size for all fibre types due to denervation. Pellegrino and Franzini (1963) indicated that there was a decrease in size of 40 to 55% of all muscle fibres after two months of denervation in the rat gastrocnemius. Similar observations have been presented by Sunderland and Ray (1950), and Miledi and Slater (1969). Although these studies did not indicate the percentage changes in muscle fibre size of the individual fibre types, these authors did demonstrate that an individual fibre was reduced by approximately 70% in its cross-sectional area.

Histological examination of the sedentary and denervated tissue sections showed that large amounts of connective tissue were present in the denervated sections, while virtually nonewas found in the sections of sedentary muscle (PLATES 8a and b). Connective tissue is evidently synthesized around the individual muscle fibres.

The findings of this investigation lend support for those presented by Sunderland and Ray (1950). It was observed that the intervals between the atrophied muscle fibres of the denervated sections were occupied by a thickened band of connective tissue, the endomysium. Therefore, it is concluded that denervation results in a progressive deposition of connective tissue around the atrophying muscle fibres and at no time was it observed that the growth of connective tissue resulted in any disorganization of the internal architecture of the muscle fibres themselves.

There were differences between the staining properties of the denervated and sedentary muscle sections during the histological examination for connective tissue (PLATES 8a and b). This inconsistancy was observed in the intensity of staining of the individual muscle fibres. In the sedentary tissue sections the majority of muscle fibres stained yellow

with only the peripheral muscle fibres staining red (PLATE 9a). On the other hand, the denervated tissues demonstrated that the majority of the muscle fibres stained red while just the central regions of the section stained yellow (PLATE 9b). The differences between the intensity of staining of the sedentary and denervated tissues could not have been due to inconsistencies in the staining procedure because both tissue types were processed simultaneoulsy. Davenport (1960) stated that the Mallory trichrome stain was composed of three different stains, and that the different rates of transmission of these stains across tissue sections might result in different degrees of staining within individual tissues. Furthermore, he suggested that the peripheral areas of a tissue section would demonstrate a more intense degree of staining. Thus differences in staining intensity of tissue sections should be expected when employing the Mallory trichrome stain. The question still remains as to why the denervated muscle tissue demonstrated large differences in staining properties. The answer may lie in the discussed fact that denervation results in the integration of the different fibre types through the attack and elimination of the characteristic enzyme systems or it may simply be the result of incomplete fixation.

C. MECHANICAL PROPERTIES OF COMPONENTS OF THE LINEAR AND NON-LINEAR MODELS

A feature of isometric contractions inherent in this study but not generally found in dynamic experiments is the change in activation of the muscle from zero to maximal. It is felt that changes in the state of activation are the underlying factors responsible for the mechanical responses of the CC and SEC during the early stages of force production. For this reason the mechanical properties of these components of muscle are

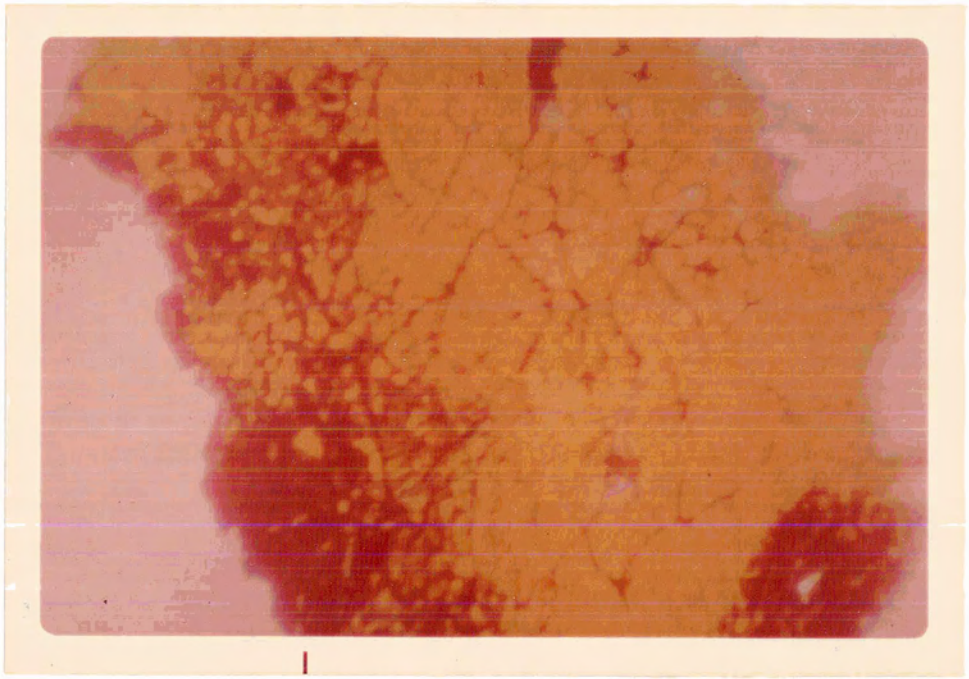
PLATE 9:

The results of the histological technique involving the Mallory trichrome stain for connective tissue.

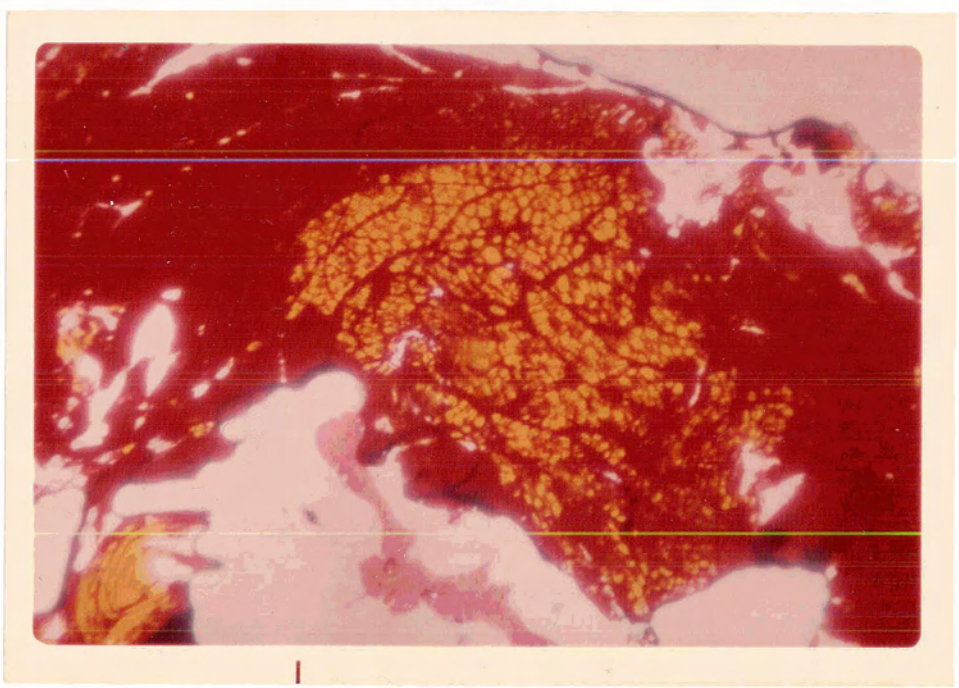
a) Sedentary muscle tissue section. Magnification 134x.

b) Denervated muscle tissue section. Magnification 134x.

a



b



described as being uniquely different than those determined under dynamic conditions.

i) The Contractile Component

a) The Force-Velocity Relationship

1) The Linear and Non-Linear Relationships

Figure 11 shows the calculated linear and non-linear F/V relationships of a number of rat gastrocnemius that made up the sedentary group. It can be seen that each of the five muscles demonstrated a non-linear F/V relationship with approximately the same shape. The mean value curve expressed the unique shape of these F/V relationships in a much more clear and precise manner. A rapid rise in velocity of shortening of the CC was observed at relatively low forces. This rise in velocity can be seen to terminate at a peak velocity near 15% of the maximal force produced (P_o) (Figure 14). The velocity of shortening of the CC then gradually decreased as the force of contraction increased. This general shape for the F/V relationship of the CC has been described in the literature as being indicative of that relationship acquired from isometric contractions (Parmley et al. 1970, 1973; Grood, 1975).

For years it was assumed that the F/V relationship of the CC produced during isometric contraction was identical to that acquired under dynamic conditions. It was not until Parmley et al. (1970) presented their results for isometric contractions that these expectations were put to rest. These authors suggested that the unique shape of the F/V curve of the CC demonstrated the effects of at least one prominent factor which could not be measured or indicated during dynamic contractions. They suggested that the initial rise in velocity of shortening of the CC observed during isometric contraction was due mainly to the rise in the

state of activation of the muscle. Jewell and Wilkie (1958) estimated that the maximum state of activation was reached approximately 60 msec. after commencement of stimulation in frog muscle at 2°C. It was estimated for the isometric contractions of the sedentary muscles in this study that maximum activation of the muscle was reached 20 to 35 msec. after the start of stimulation. These values were obtained by assuming that the rise in the velocity of shortening of the CC was due totally to the rise in activation of the muscle and therefore the highest level of velocity attained would correspond with the reaching of the maximum eventual level of activation. It was observed that these estimates were not comparable with those found by Jewell and Wilkie (1958). The differences between these results could have been the consquence of a number of factors including the use of a different animal and muscle, the size of the muscle, a difference in the level or degree of transmission of stimulation throughout the muscle, and the temperature of the muscle. These differences suggest that the validity of the above mentioned assumption should be questioned as well as the comparability of the rise-time to maximum activation of muscles from different animals.

Several other factors have been presented in the literature as possible, partial causes of the observed increase in velocity of shortening of the CC at low forces during isometric contractions. Parmely et al. (1970) speculated that there might have been a better synchronization of force-generating cross-bridges in dynamic contractions which would augment velocity of shortening at a given load. Similarly, Grood (1975) suggested that the compliance residing in the cross-bridges reacted differently in isometric and dynamic contractions. Both groups of authors implied that a direct relationship existed between the mode of contraction and the

mechanical properties of the cross-bridges. They obtained support for their conclusions from the observed fact that during isometric contractions lower velocities of shortening of the CC were developed throughout a full range of force than during dynamic contractions.

Another factor which has been suggested to have a limited effect on the velocity of shortening of the C C during the initial stages of force development was the internal friction or viscosity of the muscle (Blange, 1972). In the analysis of dynamic contractions the effects of internal viscosity of the muscle would not be prevalent because the muscle is totally activated, shortening at a constant velocity against a given load when the velocity of shortening is measured. In contrast, the analysis of isometric contractions involves the use of the complete process of force development from zero to P_o. Therefore, the effects of internal viscosity must be overcome in the initial stages of force development before the velocity of shortening of the CC is allowed to increase to maximum.

It seems likely that the initial rise in velocity of shortening of the CC during isometric contractions may be due to a complex combination and no just one of the discussed factors. Evidence presented to date suggested that the rise in activation of the muscle during isometric force-production tends to play a dominant role in the determination of the velocity of shortening of the CC during the early stages of force production. The role of cross-bridge synchronization on velocity of shortening of the CC during isometric contraction is not clear. If the cross-bridges were not synchronized at the onset of stimulation it would seem likely that they would become so soon after activation. However, the results of Parmley et al. (1970) indicated that the velocity of shortening was lower in isometric than in dynamic contractions for a

full range of loads. Therefore, if cross-bridge synchronization was not the factor affecting this depressed level of velocity during isometric contraction then another factor must be responsible.

Grood (1975) demonstrated that the relative filament velocity was dependent on the mode of contraction where there was a sudden increase in velocity of shortening in an isometric-to-dynamic changeover and a sudden decrease in the reverse process. Many authors have observed the fact that the velocity of shortening of the CC during isometric contractions was lower than that obtained during dynamic contractions, but they have not shown this repeatable changeover in the magnitude of velocity when the mode of contraction was instantaneously changed. Grood (1975) concluded that the compliance residing in the cross-bridges played an intricate part in the velocity response of the CC for any given load or mode of contraction.

The non-linear F/V relationship of the CC of rat gastrocnemius produced during isometric contractions is similar in shape to those presented by other authors. Furthermore, it is suggested that the unique shape of this relationship is the result of a combination of factors which are unique to isometric contractions. Although the shape of the isometric non-linear F/V relationship, beyond the observed peak velocity, was similar to those obtained during dynamic contractions, a number of authors have observed that the level of velocity of shortening is lower in isometric than in dynamic conditons. It is concluded that the depressed velocity levels observed for isometric contractions are the direct result of the compliance of the cross-bridges.

The linear F/V relationships for the individual muscles in the sedentary group indicated a fair representation of the non-linear relationships (Figure 11). One of the major faults with any process involving linearization

is that the finer points or distinct characteristics of any non-linear system are overlooked. Indeed, it was observed that this was the case in the present investigation. Through the process of linearization, little, if any of the unique behavior of the CC during isometric contraction can be observed. In fact, only by comparison of the linear F/V relationships obtained from dynamic and isometric contractions could any realistic conclusion be made about differences in properties of the CC for these modes of contraction. Although this comparison was not performed in the present investigation, it has been speculated that differences would be observed between the values of B of the linear F/V relationship obtained from the two modes of contraction. This speculation was brought about by the fact that the velocity of shortening of the CC of the non-linear relationships have been observed to be much lower in isometric than in dynamic contractions for a full range of force (Parmley et al., 1970). Therefore, it was concluded that the linear model should demonstrate the different effects of the compliance of the cross-bridges on the F/V relationships acquired through the use of different modes of contraction, but that the effect of a rising activation state and internal viscosity could not be separated from those of the cross-bridges themselves. Thus, as could be expected, specific characteristics of the non-linear F/V relationship were lost or forfeited for the simplicity of analysis presented by the linear model and the process of linearization.

2) Effects of Denervation and Training

The shapesof the non-linear F/V curves were similar for all the experimental groups whereas the linear relationships were observed to provide good approximations of the non-linear curves for all but one group. The effects of both training and prolonged denervation on the F/V relationship

were similar for both the linear and non-linear model.

The similarities between the sedentary and denervated (sub-groups 1 and 2) groups were limited to the relative shape of the curves. Comparison of the mean maximum force (P_o) and peak velocity of shortening of the CC for these groups indicated large differences between groups (Appendix 5; Figure 14). Sunderland and Ray (1950), Pellegrino and Franzini (1963) and Miledi and Slater (1969) all concluded that denervation was characterized by progressive fragmentation and digestion of myofilaments resulting in reduced volume of the individual fibres. It has been assumed for a long time that the production of force by muscle was closely related to interactions between the myofilaments (Huxley, 1969). Therefore, the observed decrease in MW due to fragmentation and digestion of myofilaments would be indicative of a reduced level of interaction between the muyfilaments and thus a reduced ability to produce force. Comparison of the denervated groups and the sedentary group showed that this was exactly what occurred.

It was earlier suggested that the most dramatic and variable changes in muscle due to denervation occurred during the first month of denervation and that during subsequent months the changes should stabilize becoming progressively smaller. This suggestion gained additional support when the mean values of P_o of the denervated groups were examined as a percentage of mean P_o of the sedentary group (Figure 14). It was found that during the first month of denervation the mean P_o of the denervated group was reduced by 91% representing only 9% of the mean P_o of the sedentary group. This was followed by an additional 6.3% reduction in mean P_o after 2 months of denervation which indicated that the mean P_o of this group was just 2.7% of the mean P_o of the sedentary group. These

findings indicated that an abrupt slowing of the effects of the degenerative process on force production occurred during the second month of denervation. Sunderland and Ray (1950) indicated that denervated opposing muscles were still visibley distinct indentities and that myofilaments were still prominent in the tissue. They concluded that at no time would denervated muscle lose its capacity to produce force. The findings of the present study provide some additional support for these conclusions.

Beyond the assessed differences in mean P_o, definite differences in the velocities of shortening of the three groups were observed. Analysis of the mean peak velocities of the non-linear F/V relationships of the sedentary and denervated groups showed that there were significant differences between the three groups at an -level of 0.01. It was observed that these significant differences were not limited to the mean peak velocities but that for any coinciding increment of force, the velocity of shortening of these groups differed quite significantly (Figure 14).

Investigations using only the mean peak velocity of the three groups showed that the degenerative effects of denervation after two months were greater on velocity of shortening than on mean P_o. It was found that after one month of denervation the mean peak velocity was reduced by 85% indicating that the mean peak velocity of the denervated group 1 was 15% of the sedentary groups mean peak velocity (Figure 14). Consequently, the changes in mean peak velocity was less that those found for the mean P_o after one month of denervation. The interesting results were found after two months of denervation where it was found that there was an additional decrease in mean peak velocity of 14.6%. This decrease indicated that the mean peak velocity of shortening of the

denervated (sub-group 2) group was 0.4% of the mean value of the sedentary group (Figure 14). Therefore, the slowdown in the effects of denervation was more marked on the velocity of shortening of the CC than on P_o during prolonged denervation. Furthermore, this observed effect of denervation may be indicative of a much greater effect on the enzymatic activity of muscle rather than on myofilament concentrations during advanced stages.

Barany (1967) showed that the speed of shortening of a muscle was related to the activity and concentration of myosin ATPase present, where low levels indicated slow muscle while higher levels represented faster muscle. Myosin ATPase is an enzyme thought to be closely involved with the myosin filaments. Therefore, fragmentation and digestion of myofilaments during denervation would result in reduced levels or concentrations of myosin ATPase and thus would result in the decreased speed of shortening of the CC.

Davies (1963) suggested that myosin ATPase played a major role in breaking the actin-myosin cross-bridges by hydrolyzing ATP. Therefore, in the present study, reduced concentrations of mitochondria as indicated by reduced activity of succinate dehydrogenaze would suggest that there was decreased ability to supply ATP which would indirectly result in reduced myosin ATPase activity. In this way, the histological results of the present study indicated that the activity of the myosin ATPase would be further hampered resulting in an added factor which might affect the speed of shortening of the CC.

Edgerton et al. (1969) presented additional information relating to the significant effect of denervation on speed of shortening of the CC. They determined that red and white muscle fibres in rat gastrocnemius were fast contracting fibres while intermediate muscle fibres were slow.

The present study showed through reduced fibre composition and size that the white muscle fibres suffered the most extensive damage of the three fibre types during a two month period of denervation. These results alone would suggest a dramatic reduction in the speed of shortening of the CC in denervated muscle.

An additional observation made was that the peak velocity of shortening of the CC was reached at lower levels of force as the effects of denervation progress (Figures 8, 9 and 11). It was concluded that these reductions were indicative of decreases in the time to total activation, internal viscosity and cross-bridge compliance all of which were found to be closely related to the number of active muscle fibres and their component myofilaments.

The denervated (sub-group 3) group demonstrated a unique experimental situation which presented some very interesting results and therefore required some special attention. In this group the anterior muscles were denervated instead of the posterior muscle (ie., the gastrocnemius and soleus) in which case the mechanical properties of the gastrocnemius should have been unchanged. Figures 10 and 14 showed that this was not the case. These figures indicated that there was a significant reduction in the complete dimensions of the F/V relationship of the CC. Estimates for P_o and the peak velocity showed that the reduction was approximately 50% of the sedentary group's mean values.

Referring to earlier sections of the discussion, it was shown that this group demonstrated a reduction in ML. This decrease in ML was suggested to occur because of the loss of function of antagonistic muscles. These antagonistic muscles would have normally maintained a particular ML which was advantageous to the whole system. Therefore, it was suggested that

without the presence of a functioning antagonistic muscle group, the gastrocnemius and soleus muscles were free to shorten over a period of time. The final result was that at the time of experimentation the resting length of the muscle was much shorter than the mean ML of the sedentary group.

The shortened ML and the corresponding mechanical responses of the CC of this group presented a precise indication of the relationships between force, velocity and ML. Bahler et al. (1968) showed that there was a F/V relationship which was unique for any specific ML. At first it was thought that the denervated (sub-group 3) group represented a muscle functioning at a different ML. However, the results of these authors were obtained from normal muscles. Therefore, the results of Bahler et al. (1968) demonstrated the mechanical behavior of normal muscle functioning at different ML's. In contrast, Tabary, Tabary, Tardieu and Tardieu (1971) examined the states of prolonged, forced extension and shortening on skeletal muscle. They found that extended periods of immobilization in the shortened position resulted in decreased numbers and size of the sarcomeres in muscle. Their results suggest that the mechanical properties of muscles which have undergone prolonged periods of immobilization should reflect the changes observed in the sarcomeres. Thus it is suggested that the denervated group (sub-group 3) presented a F/V relationship which demonstrated the changes in the mechanical properties of a muscle which has undergone a prolonged period of immobilization in a shortened ML.

Two trained groups were examined in this study. The first, trained sub-group 1, consisted of two rats which were examined while under the influence of the respiratory disease, pneumonia. The other trained group, sub-group 2, consisted of four healthy animals. It was found that the dimensions of the mean F/V relationships of the two trained groups were

quite different. The healthy trained (sub-group 2) group demonstrated much greater levels of velocity of shortening and P_o production than the unhealthy trained (sub-group 1) group.

It was shown that the MW's of both trained groups were comparable and when combined, their mean MW's were found to be significantly larger than the sedentary group's mean MW at an α-level of 0.01. Similar results were found for the ML's of the two trained groups; although, it was shown that no significant difference was present between themean ML's of the sedentary and combined trained groups. The similarities in the anatomical measurements of the two trained groups indicated that prolonged periods of training had the same effects on both trained groups. It was previously mentioned that these similarities were not indicated by the F/V relationships of the CC of the two groups. Therefore, it is concluded that the pneumonia had a significant effect upon the mechanical response of the CC which was not indicated by the anatomical measurements.

Gordon et al. (1969) showed that force production was directly related to myofibrillar protein concentrations while the velocity of shortening of the muscle was proportional to sarcoplasmic protein concentrations. The trained (sub-group 1) group demonstrated a 38% reduction in both mean peak velocity and P_o which may have been related to a decrease in the concentrations of both myofilament proteins and sarcoplasmic proteins. In addition, pneumonia may have reduced the transport of oxygen to the muscle, indirectly decreasing the activity of the oxidative phosphorylation process and/or possibly reduced glycogen stores within the affected muscles. The stress syndrome may also have accounted for the reduced activity in that this system increases the secretion of adrenal corticoids which results in slow metabolism of the contractile proteins. These possibilities were

assumed to be highly likely; however, to make any definite conclusions, histochemical, biochemical and histological examinations would have been necessary to compare both trained groups.

The effects of training on the mechanical properties of the CC were observed by comparing the F/V relationships obtained from the sedentary and trained (sub-group 2) groups. The F/V relationships of the CC for these groups were found to be almost identical for forces above 500 gm. while below this force level there were large differences. It was suggested in previous sections that the rise in velocity to a peak level of the CC at low force levels can be attributed to a complex combination of the effects of the compliance of the cross-bridges, the rising activation state and internal viscosity of the muscle. Figure 14 shows that the mean peak velocity of shortening of the CC was reached at a lower force for the trained (sub-group 2) group than the sedentary group. This indicates that the training procedure used in the present study had an affect on one or more of these factors. It is suggested that these differences were probably the result of changes in the rate of activation of the muscle.

Comparison of the individual F/V relationships of these groups with the computed mean value curves indicated that the peak velocity of shortening of the CC was a much more distinct entity in the trained (sub-group 2) than in the sedentary group. The training program used in the present investigation tended to refine the process of velocity development of the CC at lower forces which resulted in a more consistent rise and accented peak velocity of the shortening of the CC for the trained animals.

Gordon et al. (1967) suggested that increases in sarcoplasmic

protein concentrations would result in increased velocity of shortening and increased endurance of the muscle. They defined sarcoplasmic proteins as being representative of the enzymes involved in energy liberation. Therefore, increased concentrations of these enzymes would result in an increased ability to supply ATP which is necessary to form or break actin-myosin cross-bridges and thus accomodate an increased turnover of ATP and cross-bridges. It is concluded that the increase in velocity of shortening of the CC as demonstrated by the mean peak velocity, was the direct result of increased sarcoplasmic protein concentrations and that this increase was indicated by the increase in mean MW of the trained group. Additional support for this conclusion was obtained from the investigation performed by Barany (1967), where he showed that there was a direct relationship between myosin ATPase activity and velocity of shortening of a muscle.

Close examination of the whole mean non-linear F/V relationships for both the sedentary and trained (sub-group 2) groups indicated that the two curves were almost identical in the course they followed for forces greater than 600 gms. This can be explained by the MW results of the present investigation and those results presented by Huxley (1958). Huxley (1958) has shown that P_o corresponded to the maximum number of activated cross-bridges for a given muscle length, and that for the upper portions of the dynamic non-linear F/V relationship there was a close relation between the numbers of cross-bridges and the force produced at a given velocity.

Training was shown to increase mean MW significantly and this was suggested to be the result of an increase in the energy liberating enzymes in the muscle (sarcoplasmic proteins). AT no time was there any indication of an increase in the myofibrillar proteins which suggests that there was no increase in the number of available cross-bridges. These findings

show that there should have been little difference in the number of available cross-bridges between the sedentary and trained (sub-group 2) muscles and that this would suggest that there should have been little difference in the non-linear F/V relationships of these groups at high forces. It is concluded that these observations gained unquestionable support when the graphic results of the non-linear F/V relationship for these groups were examined.

3) Comparison of the Linear and Non-Linear Relationships

It was shown that significant differences existed between the non-linear F/V relationships of the denervated sub-groups 1 and 2 and the sedentary group. Examination of the individual F/V relationships for these groups indicated that the linear relationships gave a good approximation of the non-linear curves for the individual animals that made up these groups (Figures 8, 9 and 11). Statistical anlaysis of the mean slope (B), P_o and maximal velocity (V_{max}) showed that the linear F/V relationships for the denervated groups were significantly different from those of the sedentary group at an α-level of 0.01 (TABLES 11, 12 and 13). Therefore, it was concluded that the linear model indicated the significant effect of prolonged denervation and gave a good approximation of the non-linear relationship of the denervated groups.

A number of inconsistencies were observed to occur between the linear and non-linear F/V relationships of the various experimental groups. Previously it was reported that prolonged denervation was observed to affect the mean peak velocity of the non-linear F/V relationship more than mean P_o. The mean linear F/V relationships of the denervated groups did not substantiate this observation and in fact, suggested the opposite (Figure 15). The mean linear F/V relationships of the sedentary and trained

(sub-group 2) groups were observed to provide a fairly good representation, but some doubt arose as to their comparability with the non-linear F/V relationships for these groups.

It was suggested that a good linear representation of a non-linear curve would be one that demonstrated the same area under the curve. The mean non-linear F/V relationships of the sedentary and trained (sub-group 2) groups were integrated to determine the area under each of the curves. The theoretical mean linear F/V relationship calculated for both groups was shown to indicate V_{max} values which were approximately 20% lower than the values produced by the linear model (Figure 31). This overestimation of V_{max} shows that the theoretical mean B values were therefore higher than those produced by the linear model. Therefore, it was concluded that the linear model produced overestimations of V_{max} and underestimations of B for the F/V relationships of all the experimental groups. It was observed that these discrepancies would account for the conflicting results presented by the linear and non-linear F/V relationships of the denervated groups.

At first these results were quite surprising but the explanation was found after examining the original assumptions of the linear model. This model assumed that the force generator (Fm) was maximally activated instantaneously. This assumption held true for dynamic contractions where the muscle was totally activated at the time velocity of shortening was measured. The analysis of isometric contractions, on the other hand, involved the total development of force from an inactivated to a totally activated state. Therefore, the isometric myogram showed a slow rise in force just after the onset of stimulation which then rose steeply before gradually slowing as maximum force production was approached. To accomodate

the initial assumption of the linear model, that the force generator reacted instantaneously, the early rise in force was neglected by continuing the steep portion of the isometric to the time axis and thus producing the desired exponential curve (Figure 34). Therefore, the estimated time taken to reach 63.2% of maximal force was lower than the real value for the isometric force development. This difference was found to be responsible for the 20% overestimate of the calculated linear mean F/V relationships for all the experimental groups. It is concluded that these overestimates must be expected if the linear model is used to analyze isometric contractions in the present form.

Although there were some inconsistencies in the SD's of the linear and non-linear F/V relationships, both relationships were shown to indicate significant differences in the F/V responses of the CC of muscles denervated for an extended period of time. This conclusion could not be made when the linear and non-linear F/V relationships of the trained (sub-group 2) group were compared. The significant differences indicated by the linear parameters were not as prevalent in the non-linear mean F/V curves of the sedentary and trained (sub-group 2) groups. Although there was a definite increase in velocity of shortening of the CC at low forces of the trained group, the SD's of the non-linear F/V relationship were so large that the differences were not significant. The large SD's of the non-linear mean F/V curve were more probably the direct result of the non-linear system of analysis and the small number of experimental animals in the group. Therefore, it was concluded that the linear system of analysis would be better than the non-linear for purposes of determining the overall effect of an experimental treatment because of its simplistic interpretation of the raw data.

Only one group presented linear and non-linear F/V relationships that were obviously not comparable. The denervated sub-group 3 showed that the linear F/V relationship bore little resemblance to the non-linear curve (Figure 10). No definite conclusions could be made about this unique result because the group consisted of only one animal.

b) The Isometric Force-Length Relationships

1) Effects of Prolonged Denervation, Disuse and Training

Figures 16 and 17 indicated that the CC of the denervated groups exhibited F/L relationships with the expected shape which has been explained in terms of the area of overlap of the myofilaments. It was observed that there was a rise in force which leveled off forming a plateau where maximum contractile force was developed. This plateau occurred at ML's greater than L_o. Comparing the F/L relationship for the sedentary, denervated and trained groups showed that the actual shape of this relationship for all the groups were quite similar. Between group differences were found to be present in the magnitude of the curves and ML's where the force produces by the CC approached zero beyond L_o.

It was previously mentioned that denervation resulted in the progressive fragmentation and digestion of the myofilaments which effectively reduced the number of available cross-bridges and thus the force that was produced by the muscle. The effects of progressive fragmentation and digestion of myofilaments were clearly shown by the mean F/L relationships of the denervated groups when compared to the sedentary groups. It was observed that the force plateau of the denervated (sub-group 1) group was reduced to approximately 20% of the maximum force plateau of the sedentary sub-group 2 and that the magnitude of force produced by the denervated (sub-group 2) group was reduced to only 5% of the sedentary level (Figure 30).

These results provided further evidence to support the conclusion that prolonged denervation drastically reduces the contractile capabilities of skeletal muscles. Furthermore, it was observed that the suggested slowing of the degenerative processes as the period of denervation progressed was evident in the F/L relationships of the CC when the denervated groups were compared to the sedentary groups.

There was some evidence to suggest that denervation affected the functioning range of length of the CC. It was observed that the muscle length at which the force produced by the CC approached zero became progressively closer to L_o as the period of denervation increased (Figure 30). Similar results were found to occur with age as was indicated by the two sedentary groups. These findings suggested that the changes in the relationship between ML and zero force production of the CC was the result of changes in the mechanical properties of the PEC. It was shown that in the case of prolonged denervation and disuse there were marked increases in the stiffness and range of the PEC (TABLE 15).

Figures 18 and 19 presented the F/L relationships of the PEC and CC for sedentary groups tested two months apart (sub-groups 1 and 2). This two month separation was observed to result in an increased ability of the CC to produce force for the sedentary sub-group 2 for ML's below L_o where a maximum force plateau exists for rat gastrocnemius. Furthermore, the sedentary sub-group 2 demonstrated a much more rapid decline in force for lengths greater than L_o (Figure 21).

The increased level of force produced by the sedentary sub-group 2 for the muscle lengths corresponding to the maximum force plateau of the F/L relationship of the CC was attributed to proliferation of the contractile processes. This means that the older sedentary group probably had better

development and utilization of the myofibrillar and sarcoplasmic proteins or perhaps even increased concentrations of these proteins.

Figure 20 showed the F/L relationships of the trained group. It was found that the CC of the trained groups produced a somewhat greater level of force on the maximum force plateau but that this increase was not shown to be significant. The force level declined rapidly for muscle lengths greater than L_o and this decline was found to follow almost the same course as was exhibited by the sedentary sub-group 2 (Figure 21). These results indicated that the mechanical properties of the CC, as expressed by the F/L relationships, did not change significantly with the advent of the described training program. These findings were found to be consistant with those expressed by the mean P_o values determined for the F/V relationships for these groups.

The speedy decline in force produced by the CC for lengths greater than L_o was suggested to be the result of a more prominent role played by the PEC in the sedentary (sub-group 2) and trained groups. The decline in force was found to be much more rapid in the sedentary sub-group 2 than in sub-group 1 which corresponded with a stiffer PEC in the second group (TABLE 15). These findings suggested that during aging the PEC becomes stiffer, resulting in a more prominent effect on muscle lengths greater than L_o, thus reducing the effects of the CC at those lengths.

ii) The Series Elastic Component

a) The Compliance-Force Relationship

1) The Linear and Non-Linear Relationships

Some confusion arose when the compliance-force (C/F) relationships

of the SEC for the sedentary group fo animals were compared with those presented in the literature. Wilkie (1950) showed the C/F relationship of human muscle to have a shape somewhat similar to the isometric F/V relationship, where the compliance diminished as force increased (Figure 35). Results similar to Wilkie's have been recently obtained by Sanderson (1975). In the studies performed by both authors the mechanical evaluation of the muscular components were acquired by using the added compliance technique devised by MacPherson (1953). Therefore, the C/F results obtained by these authors should have been comparable to those presented in the present study. This was not the case.

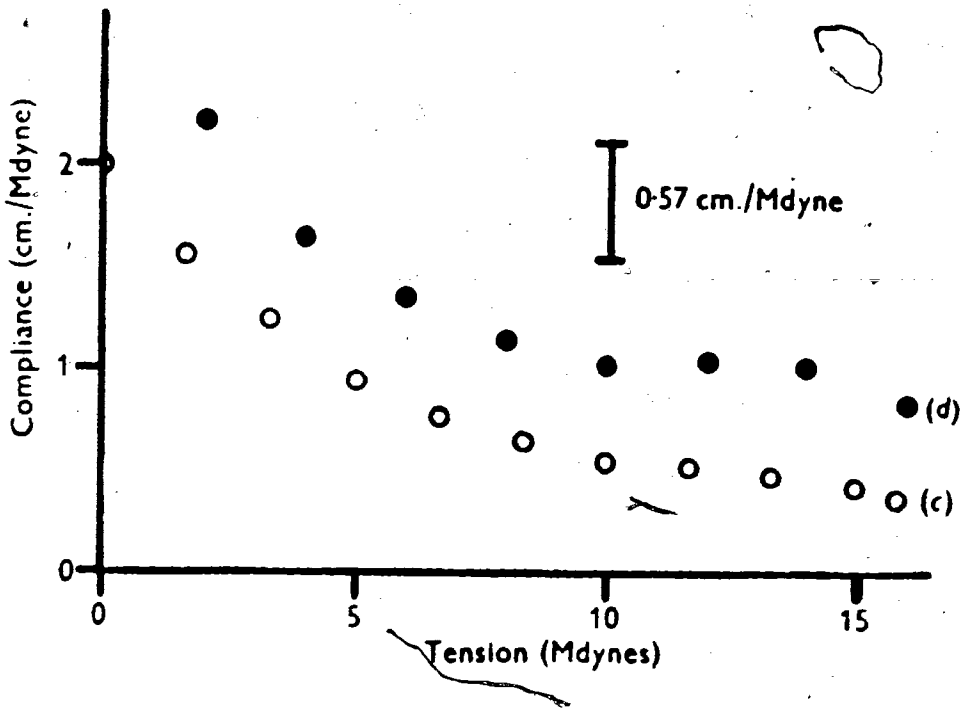
The results of the C/F relationship of the SEC of the present study indicated that the non-linear relationship was as unique as was the F/V relationship for isometric contractions. It is suggested that the non-linear C/F relationship produced from isometric contractions of normal healthy muscle in the present study can be divided into three distinct sections. These sections were described as: 1) the initial rise to a peak compliance at low forces; 2) a rapid decline in compliance to a steady level throughout the middle ranges of force and 3) an additional rapid decrease in compliance at higher forces approaching maximum isometric force.

If the cross-bridges were the major sites of the muscle's SEC compliance, then the non-linear C/F relationship would be easily explained by cross-bridge involvement as the result of length and/or activation changes of the CC. With the onset of stimulation resulting in a rising activation level, the numbers of force-generating cross-bridges were assumed to increase and therefore would result in the shortening of the CC and extension of the SEC. As the results of Huxley et al. (1971a) and

FIGURE 35:

The variation of compliance with force (tension), arm alone (C), compliance of system added (D).

(Wilkie, 1950, p. 264)


Compliance (cm./Mdyne)
2
1
0
0·57 cm./Mdyne
(d)
(c)
0
5
10
15
Tension (Mdynes)

Bressler et al. (1974) indicated, there should be a decrease in the muscle's SEC compliance which would correspond with the increased area of overlap of the myofilaments and thus increased number of cross-bridges during shortening of the CC. The general trend of the mean C/F relationship of the sedentary group exhibited the expected decrease in SEC compliance as the CC shortened but a contradiction was presented by the early portion of the curve (Figure 19).

If it can be assumed that the cross-bridges exhibit mechanical activity only upon stimulation or activation, then the initial rise in the non-linear C/F relationship found in the present study would suggest that the SEC compliance is activation dependent. This activation dependency could be interpreted in two different ways. Firstly, the initial rise in the non-linear C/F relationship may have been indicative of the increased involvement of fully activated cross-bridges where increasing chemical or electrical activity in or around each cross-bridge changed its resident compliance. The other alternative was that this rise in the non-linear C/F relationship was directly related to the increased involvement of the cross-bridges and their resident compliance and thus indicated a transition period between tendon and cross-bridge dominance in the determination of the compliance properties of the SEC. Therefore, the SEC may present properties similar to those of an inert spring during dynamic contractions but that the active involvement of the force-generating cross-bridges from zero to total activation as expressed by isometric contraction may alter these properties.

Figures 22 to 28 showed that the initial rise in SEC compliance at low forces was exhibited by all the experimental groups. Although the non-linear C/F relationships for each treatment was indicated to start

at the origin of the graph, this was definitely not the case. For each experimental group at least two values of SEC compliance were calculated which suggested a trend toward a peak level of SEC compliance. This trend was then extrapolated to incorporate the origin and thus accent the shape of the non-linear C/F relationship of the SEC obtained during isometric contraction. In actual fact, it can be assumed that at no time or condition whould biological material exhibit zero compliance. Thus, it is suggested that in actual fact the non-linear C/F relationship of the SEC was initiated from a non-activated compliance level which was larger than zero and that from this level the non-linear C/F relationship increased to a peak level at low forces with the increased involvement of cross-bridges. It could be proposed that this initial level of compliance of the SEC before stimulation could be indicative of the mechanical properties of that portion of the SEC that resides in the muscle tendons and connective tissue. Therefore, the early rise in the non-linear relationship of the SEC indicates a transitional period of changing SEC compliance which is attributed to the rising state of activation. As no direct measure of activation is possible, the only part of the C/F curve which may be considered is that which was obtained after maximal activation was achieved. This point in time is difficult to identify, it is probable that it occurred after the point where velocity began to decrease with increasing force in the F/V relationship. This point can be identified on the C/F curves as being that at which compliance was maximal.

The central regions of the non-linear C/F relationship of the SEC for the sedentary and trained (sub-group 2) groups demonstrated a distinct similarity in shape to those relationships presented in the literature for dynamic contractions (Figure 35). This investigation showed that the peak level of compliance of the SEC corresponded to the peak velocity of shortening

of the CC and this indicated that the area of the non-linear curve where maximal activation and myosin ATPase activity was reached for the whole muscle. Progressive isometric force development beyond these peak levels of velocity and compliance resulted in changes in length of the CC and SEC. These length changes were indicative of increased numbers of cross-bridges until P_o was reached. The reduced value of the velocity of shortening of the CC corresponded with smaller and smaller changes in the length of the CC and SEC. Therefore, when the force production of the CC continued to increase towards P_o, the ability of the SEC to accomodate additional increases in length began to decrease resulting in increased resistance to length changes, decreased velocity of shortening of the CC and thus decreased compliance of the SEC. It can be concluded that the mechanical behavior of the SEC was length and force dependent and that this dependency can be expressed in the form of an extension-force (E/F) relationship. Furthermore, the central region of the non-linear C/F relationship of the SEC produced during isometric contraction can be explained in terms of numbers of involved cross-bridges, where, as the number of involved cross-bridges increases, the compliance of the SEC decreases.

It was observed that as P_o was approached there was a sharp decline in the compliance of the SEC for both the sedentary and trained (sub-group 2) groups (Figure 28). The decline in SEC compliance at high forces demonstrated that the maximal extension of the SEC was being approached and that the resistance to length changes was increasing dramatically. This increased resistance or decreased compliance can be observed by examining the E/F relationship of the SEC where, at high levels of force, increasingly larger levels of force were required to produce significant length change in the SEC. Obviously factors other than the number of

involved cross-bridges affected this decline. Thus it is speculated that the maximal compliance of the cross-bridges themselves had to be attained or was being approached as indicated by the plateau region of the non-linear C/F relationships of the sedentary and trained (sub-group 2) groups, and that further force production resulted in the extension of the SEC residing in the tendons of the muscle (Figure 29). Therefore, the sharp decline in the non-linear C/F relationships observed for these groups is suggested to indicate the increasing involvement of the SEC present in the tendons. Further evidence which may support this suggestion was observed in that there was a similar terminal compliance level for a number of the experimental groups (Figure 29).

A possible method of determining the contribution of the SEC compliance of the muscle and tendon would be to acquire the non-linear F/V and C/F relationships of a muscle with and without its tendons intact. Comparing these relationships would give a good indication of the tendon's contribution to the SEC's compliance. Another possibility could be to acquire the isometric F/L relationships of a muscle with and without its tendons intact. Subtracting the isometric F/L relationships of the muscle without its tendons intact from that obtained with the tendons intact would produce the E/F relationship of the SEC that resides in the tendons. Hopefully these techniques may provide a good estimation of the SEC compliance that resides in the tendons.

Previously it was mentioned that the linear relationship gave little indication of the unique non-linear F/V relationship of the CC produced during isometric contraction. A similar statement can be made for the comparison of the linear and non-linear C/F relationships of the SEC.

Visual evaluation suggested that the linear C/F relationship was much less accurate in representing the non-linear C/F relationship of the SEC than was found for the F/V relationship of the CC. In fact, the linear representation provides virtually none of the specific characteristics of the non-linear C/F relationship which might help distinguish between a linear value obtained from dynamic or isometric conditions.

2) Effects of Denervation and Training

The denervated (sub-group 3) group presented a unique experimental situation which demonstrated quite distinct non-linear C/F results (Figure 24). Although this group consisted of only one animal, it represented a situation where the effects of denervation could be assessed on an antagonistic group fo muscles. It has been shown that the gastrocnemius was not denervated in this group and that it underwent significant passive shortening during the period of denervation of its antagonistic muscles. Furthermore, it was suggested that this shortening resulted in an increased overlap of the myofilaments and thus a reduced number of cross-bridges. This change in ML was thought to be indicated by a different non-linear F/V relationship which was dictated by the shorter ML. Eivdence to support the suggested change in myofilament overlap and number of cross-bridges was thought to be demonstrated by the much slower rise in SEC compliance at low forces of the denervated (sub-group 3). In fact, the denervated (sub-group 3) group demonstrated a slower rise in the SEC non-linear C/F relationship than both denervated sub-groups 1 and 2, while expressing approximately the same rise in compliance as the sedentary group. An obvious inconsistency was presented by these results; for if the shorter ML did in fact represent a decrease in the number of available cross-bridges, then the denervated (sub-group 3) group should have demonstrated

a rise in SEC compliance which was much slower reaching a higher peak compliance than that of the sedentary group. Thus the question arose as to the effect of a prolonged shortened state on healthy muscle.

Tabary, Tabary, Tardieu and Tardieu (1971) demonstrated that muscle immobilized in a shortened position resulted in decreased numbers and the size of the sarcomeres and thus in the numbers of available cross-bridges. Although these authors did not examine muscles shortened as a result of antagonistic denervation, their findings suggested that muscles shortened for an extended period of time undergo structural changes which should be reflected in the mechanical properties of the various components. It was concluded then that the non-linear C/F relationship of the denervated (sub-group 3) group was indicative of that relationship which should be expected for muscle which has undergone an extended period of shortened length. Consequently this group demonstrated an L_o which was shorter than the normal muscle and thus the various muscle components demonstrated properties which were effected by structural changes.

Dramatic differences in compliance of the SEC were observed between the sedentary and trained (sub-group 2) groups during the early stages of force development (Figures 25, 27 and 28). It was suggested that differences between these groups, as expressed by the mean non-linear F/V relationships, were due to changes in sarcoplasmic protein concentrations and thus the rate of activation of the muscle and alterations in the compliance of the cross-bridges. The observation was made that the peak compliance of the SEC was higher and attained at a lower force in the trained (sub-group 2) group than in the sedentary group. This indicated that the rate of rise in compliance was increased by training and was attributed to an increased rate of activation of the muscle with the advent of stimulation.

The peak levels of compliance of the non-linear C/F relationship were assumed to indicate maximal activation of the muscles as did the peak velocities of the non-linear F/V relationships. The trained (sub-group 2) group demonstrated a peak compliance which was much higher than that of the sedentary group (Figure 28). It was concluded that this increased compliance of the SEC at the onset of total activation was indicative of changes in some portions of the SEC.

The major portion of the mean non-linear C/F relationship of the SEC of the trained (sub-group 2) group was almost identical to that of the sedentary group. This suggested that the numbers of involved cross-bridges throughout the normal range of force production were similar for both groups. Podolsky and Nolan (1973) have indicated that the dynamic C/F relationship could be described in terms of the number of involved cross-bridges. There is little doubt that this observation can be applied to that portion of the isometric C/F relationship which lies beyond the peak compliance level. Considering the results of Podolsky and Nolan (1973) in conjunction with the findings of the present study, it was concluded that training resulted in virtually no change in myofibrillar protein concentrations. These observations tend to support the conclusion that the training program used affected an increase in sarcoplasmic protein concentrations. Furthermore, the similarities in the mean non-linear C/F relationships of the sedentary and trained (sub-group 2) groups suggested that the larger portion of the SEC compliance residing in the cross-bridges was unchanged. This portion of the SEC compliance was thought to be adequately described by the parallel combination of a dashpot and spring presented by Huxley and Simmons (1971a).

The trained (sub-group 1) group presented a non-linear C/F

relationship of the SEC which was different than the other trained group and was felt to be the result of the effects of pneumonia. It was suggested earlier that pneumonia may have affected any one of a number of the energy liberating metabolic processes and/or substrates, or could have facilitated the destruction of myofibrillar proteins via the Stress Syndrome. Throughout the full range of force production of this group there was observed to be a higher level of compliance of the SEC than that of the trained group (sub-group 2). Taking into account the conclusions of Podolsky and Nolan (1973) it was suggested that pneumonia resulted in decreasing the number and activity of the cross-bridges by the metabolism of myofibrillar proteins. It must be concluded that additional research involving biochemical, histological, histochemical and biochemical analyses is necessary before relevant conclusions can be made concerning the effects of pneumonia on the mechanical properties of muscle.

In all the experimental groups the linear model produced linear approximations of the non-linear C/F relationships which seemed inadequate. This inadequacy was not limited to the description of the specific characteristics but seemed to represent an overestimation of the non-linear C/F relationships. In each case the linear approximation was observed to be affected more by the peak level of compliance rather than the main body of the non-linear C/F relationship. It must be stated that although there seemed to be a consistant overestimation of the theoretical non-linear C/F relationhip by the linear model, the mean linear approximations did suggest similar trends as the mean non-linear curves which were due to the experimental treatments.

3) Comparison of the Linear and Non-Linear Relationships

The mean linear compliances of the denervated groups were greater

than those of the sedentary group at an α-level of 0.01 (TABLE 14). There was a progressive increase in the magnitude of the linear compliance as the effects of denervation progressed. This progression was also exhibited by the mean peak compliance of the non-linear C/F relationships of the denervated groups. It is concluded that the linear values indicated the trend of the non-linear C/F relationships for the denervated groups (sub-groups 1 and 2) but that the linear values seem to demonstrate a bias for the mean peak complinace levels.

The standard deviations (SD's) of the linear and non-linear mean value C/F relationships of the denervated (sub-groups 1 and 2) and sedentary groups suggested that the linear evaluations of complinace of the SEC were more consistant than the calculated increment compliances of the non-linear curves (Figure 29). It was suggested earlier and is concluded here that the linear model was much more accurate in its assessment of the isometric myograms because of its simplistic interpretation of the raw data. Although the numbers of experimental animals were small in each group, the linear estimates of compliance were still quite consistant in comparison to the individual non-linear C/F curves (Figures 22, 23 and 25). Therefore, it was concluded that the much larger SD's observed for the non-linear C/F curves of the SEC for these groups were the direct result of experimental errors in determining the shape of the isometric myograms at equal increments of force.

As was observed for the F/V relationship, the denervated (sub-group 3) group demonstrated a unique result when comparisons are made between the linear and non-linear C/F relationships. The non-linear C/F relationship of the denervated sub-group 3 indicated that the compliance level of the SEC was lower than the sedentary group mean value C/F relationship (Figure 28).

However, the linear estimate of compliance suggested that the compliance of the SEC was higher than the sedentary linear mean C/F relationship for the full range of force production (Figure 28). No definite conclusion could be presented for these results because the group consisted of only one animal. As previously suggested, the linear model seemed to have difficulty in reflecting the effects of decreased ML's less than L_o. In fact, it was speculated that L_o was shifted to a value lower than that of the sedentary group's and that this shift resulted in changes in the internal structure of the muscle (Tabary et al., 1971). Therefore, it could be suggested that the linear model lacked the ability to demonstrate changes in the mechanical behavior of healthy muscle suffering the effects of prolonged reduced ML's.

The linear mean C/F relationship of the trained (sub-group 2) group indicated a similar increase in compliance over the sedentary value as did the denervated groups (Figure 29). Although the increase was not as dramatic as in the denervated groups, it was found to be significantly different from the sedentary linear mean value at an α-level of 0.05 (TABLE 14). This significant difference was not evident when the non-linear mean C/F relationships were compared for the sedentary and trained (sub-group 2) groups (Figure 29). It was suspected that a significant difference may have existed at low force between the mean non-linear C/F relationships of these groups, but only one point -- the peak compliance -- indicated that this was true. The remainder of mean non-linear C/F relationships of these groups demonstrated absolutely no difference. Therefore, it was concluded that changes in compliance of the non-linear C/F relationships of the SEC during the early stages of force development played a prominent role in the determination of the linear compliance

displayed by the linear model.

The SD's determined for the non-linear mean C/F relationships of the sedentary and trained (sub-group 2) groups were of such a magnitude that it was difficult to suggest that there were significant differences for any portion of the curves. It was suggested that a significant difference existed between the mean non-linear C/F relationships of these groups at low forces but the SD's of only one point of the curves supported this suspicion. There was no doubt in the results of the linear mean values for these groups (Figure 29). The SD's of the linear mean values of compliance of the SEC were such that there could be no doubt that the differences were significant for these groups. As in the mean F/V results for these groups, it must be concluded again that the linear system of analysis presented a much simpler method of assessing isometric myograms. This simplicity was reflected in terms of experimental error and thus the SD of the mean C/F relationships.

b) The Extension-Force Relationship

1) The Linear and Non-Linear Relationships

The E/F relationships of the SEC were determined by integrating the mean C/F relationships of the major experimental groups (Figure 30). These relationships were found to be as unique to isometric contraction as were the C/F and F/V relationships. To date, the isometric E/F relationship of the SEC has not been examined in great detail. The general impression obtained from the litereature was that the isometric E/F relationship was the same as that obtained during dynamic contractions. Observing the E/F relationship of just the sedentary group showed that this was not legitimate assumption. In fact, unlike the dynamic E/F relationship, the isometric relationship demonstrated a slow rise in extension

of the SEC at low forces. This would suggest that the mechanical response of the SEC was activation dependent in the early stages of isometric force production.

The overall trend of the E/F relationships of the SEC during isometric contractions was similar to those acquired by dynamic contractions. The only difference in shape observed was present in the early stages of force development where there were relatively small changes in length of the SEC. This portion of the curve corresponded to the early rise in compliance. Thus it was concluded that this early portion of the E/F relationship indicated the introduction and increased involvement of the cross-bridges. One total activation was reached, the isometric E/F relationship of the SEC resembled that produced during dynamic contractions.

Similar conclusions can be made concerning the comparability of the linear and non-linear E/F relationships as were presented for the F/V and C/F comparison of those relationships. Obviously specific characteristics of the non-linear relationship were sacrificed by the linear model for the purposes of simplicity. There was some suggestion that the linear E/F relationships gave a better indication of the non-linear relationships than did any of the previous linear parameters. Even then, the linear isometric E/F relationship would be hard to distinguish from one produced during dynamic contractions due to the lack of specific information which was provided by the non-linear E/F relationship of the SEC.

2) The Effects of Denervation and Training

The denervated groups demonstrated a progressive decrease in the magnitude of length changes during isometric force production (Figure 30). There were significant decreases in mean P_o which was equated with the effects of the degenerative processes characteristic of prolonged denervation.

Podolsky and Nolan (1973) suggested that the number of active cross-bridges had a direct effect on the compliance of the SEC. It is suggested in the present investigation that there was a progressive reduction in the number of cross-bridges resulting from denervation. In addition, there were definite increases in the slope of the E/F relationships of the denervated groups when compared to the sedentary groups. Thus, it was concluded that the increase in slope of the E/F curves observed for the denervated groups are representative of the progressive decrease in the number and activity of involved cross-bridges which was indicated by the reduced level in mean P_o.

The initial portion of the sigmoid E/F curves of all the experimental groups suggested that there were definite changes in the mechanical properties of the SEC during the onset and development of activation. These early changes were attributed to the effect of a rising state of activation on the mechanical properties of the SEC. These results suggest that MacPherson's (1953) method does not apply to isometric conditions because the basic assumption made in his technique is violated.

An interesting relationship was found to exist between mean peak velocity of shortening of the CC and the maximal mean extension of the SEC. It was found that there was an 85% reduction in both the mean peak velocity of the CC and maximal extension of the SEC during the first month of denervation (denervated sub-group 1). After two months of denervation the additional reduction in extension of the SEC and velocity of shortening of the CC were found to be similar for both these parameters. It is concluded that the maximal extension of the SEC was velocity dependent. This conclusion suggests that extension of the SEC was directly related to the effects of the numbers and activity of the cross-bridges on the

compliance properties of the cross-bridges themselves or the tendons.

It was shown that there was a significant increase in the amount of connective tissue around the muscle fibres after two months of denervation. If this increase was indicative of increases or changes in the amount of connective tissue in the tendon then it could be suggested that there would be a decrease in the compliance of the SEC thus reducing its ability to increase in length. This was not found to be the case (Figure 30). It was suggested by the C/F relationship of the SEC that there was an increase in the overall compliance of the SEC thereby suggesting an increased ability to undergo length changes (Figure 28). From these results it is concluded that the level of extension reached by the SEC was closely related to the numbers and activity of the cross-bridges. This would tend to suggest that the E/F relationship accents the role of cross-bridge compliance in the determination of the mechanical properties of the SEC.

The E/F relationship of the trained groups substantiated the conclusions made in the previous paragraphs (Figure 30). The same sigmoid shape for the E/F curves was demonstrated by the trained group. As in the previous groups discussed, the initial portion of this relationship suggested that changes in the elasticity of the SEC occurred during the process of activation.

It was observed that the E/F relationship of the trained group demonstrated a high rate of length changes in the SEC with the development of force. Earlier it was shown that the increase in trained mean MW was indicative of an increase of sarcoplasmic protein concentrations and thus, energy liberation and cross-bridge activity. Coupled with the observed increase in rate of activation of the muscle, these findings suggested that the increased rate of extension of the SEC was the result of these

factors.

3) Comparison of the Linear and Non-Linear Relationships

The linear and non-linear mean C/F relationships of the SEC were integrated to produce the linear and non-linear E/F relationships of the four major experimental groups. The linear relationships were found to provide a better fit for the non-linear E/F relationships of the SEC than was observed for the other mechanical parameters of the muscle components for these groups.

Integration of the theoretical C/F relationship of the SEC for the sedentary and trained (sub-group 2) groups produced the theoretical E/F relationship for these groups. It was found that the linear mean E/F relationship demonstrated the 20% overestimation of the theoretical relationship which was observed during the comparison of the mean C/F relationships (Figure 33). There was some question as to the representation of the non-linear E/F relationships by the theoretical linear relationship for both the sedentary and trained groups. It seemed that the theoretical curves underestimated the non-linear E/F relationships but at the same time presented a fairly good indication of general trend of these relationships (Figure 33). In more precise terms, the linear mean E/F relationship demonstrated the 20% overestimation of the theoretical relationship which was observed during the comparison of the mean C/F relationships (Figure 33). There was some question as to the representation of the non-linear E/F relationships by the theoretical linear relationship for both the sedentary and trained groups. It seemed that the theoretical curves underestimated the non-linear E/F relationships but at the same time presented a fairly good indication of general trend of these relationships (Figure 33). In more precise terms, the linear model's representation was

a good indication of the E/F relationships when the individual points were examined for the non-linear E/F relationships of the SEC for these groups. On the other hand, the theoretical E/F relationships provided an adequate indication of these non-linear E/F relationships when the slope at each point was considered. It was suggested that the course, and hence the slope, of the linear E/F relationship provides a much more accurate indication of the E/F properties of the SEC during isometric contractions. Therefore, it was concluded that the linear model overestimated the trend of the non-linear E/F relationship of the SEC by 20%. Furthermore, this overestimation was believed to be the direct result of the linear system of analysis where T was consistantly underestimated (Figure 34).

iii) The Parallel Elastic Component

a) The Force-Length Relationship

1) The Effects of Prolonged Denervation, Training and Disuse

The denervated groups demonstrated a progressive increase in the slope and decrease in the length axis intercept for the mean F/L relationships of the PEC when compared to the sedentary (sub-group 1) group (TABLE 15). It was shown that denervation resulted in a significant increase in the concentrations of connective tissue around the individual muscle fibres. Thus it was concluded that the progressive increase in the concentration of connective tissue produced the observed increased slopes or decreased compliance of the PEC (Figure 21).

Histological analysis performed in the present study showed a significant decrease in the size and activity of the three types of muscle fibres found in rat gastrocnemius during denervation. It was suggested that these decreases were reflected in progressive decreases in the con-

tractile processes involved in force production. The levels of active force production were shown to decrease as denervation progressed accompanied by a less distinct transition between CC and PEC force as ML was increased beyond L_o. Thus the functional range of length of the CC was being continually reduced as denervation progressed.

Prolonged disuse produced a significant increase in the slope and decrease in the length axis intercept of the F/L relationship of the PEC of rat gastrocnemius (TABLE 15). These changes resulted in reduced extensibility of the whole muscle and a much more rapid transition between CC and PEC dominance as the ML was increased (Figure 21).

Elliott (1965) showed that tendon was composed of parallel aggregations of collagen fibres longitudinally aligned. There was a continual process of cross-link formation between the collagen fibres which were aligned in parallel (Petruska and Hodge, 1964). Some of these cross-links have been reported to be permanent while others can be broken once formed during active stretching of the tendons (Elden, 1968). It is concluded that the observed stiffening of the PEC during prolonged disuse was the direct consequence of the continual formation of the cross-link network in the connective tissue (collagen) of the tendons. Thus the progressive stiffening of the PEC reduced the dominance of the CC for lengths much greater than L_o thereby decreasing the functioning range of the CC (Figure 21). These decreases were expressed by a more distinct transition from CC to PEC dominance in static force production as the ML was increased.

Training was observed to induce a similar increase in the slope of the mean F/L relationship of the PEC as was demonstrated by the denervated (sub-group 1) group (TABLE 15). However, the functional range of ML of the trained group was reduced far more drastically than that exhibited

by the denervated (sub-group 1) group (TABLE 15). Training produced a stiffening of the PEC which reflected a reduced involvement of the CC for lengths greater than L_o. This stiffening effect may have been due solely to the training procedure or to the natural process of aging or to both. Comparing the mean F/L relationship of the PEC of the trained and sedentary (sub-group 2) groups showed that the curves differed very little. No conclusions could be drawn from these results because the experimental groups comprised only two animals. It was suggested that training had virtually no effect on the F/L relationship of the PEC due to the fact that there was no obvious differences in the force production of the CC between the sedentary (sub-group 2) and trained groups.

Examination of the values of compliance obtained for the PEC of the various groups produced a very interesting correlation. It was observed that the compliance of the PEC of the sedentary (sub-group 1) and trained groups bore an extremely close resemblance to the compliance exhibited by the plateau region of the non-linear C/F relationships of the SEC for these groups. It was concluded earlier that the non-linear C/F relationship of the SEC at higher forces demonstrated the increasing involvement of the SEC compliance residing in the tendons. This increased involvement was thought to occur as the compliance of SEC that resides in the cross-bridges approached that of the tendons. The similarities in the PEC and SEC compliance at these higher levels of force seem to substantiate the above conclusion for the sedentary and trained (sub-group 2) groups. These similar results could be purely accidental but they suggest that the compliance that resides in the cross-bridges could be equated with that of the fascia of the muscle at high forces because the compliance of the tendons were common for both methods of data acquisition (ie.,

F/L and F/V study).

From these results it was thought that the compliance of the tendons do not contribute to the compliance of the SEC to any significant degree for the denervated groups. This conclusion was supported by the fact that neither denervated group presented a plateau region in the non-linear C/F relationship of the SEC. Furthermore, the non-linear C/F relationship of the SEC for these groups probably demonstrated the compliance properties of only the cross-bridges.

iv) Justification of MacPherson's (1953) Technique

MacPherson (1953) developed a technique to determine the mechanical properties of the CC and the SEC using a pair of isometric contractions. This technique incorportated an added series compliance in half the performed isometric contractions and required that a pair of isometric contractions, one with and one without this added compliance, had the same eventual steady state. A number of problems were encountered using this technique.

The basic assumption inherent in this technique is that the velocity of shortening of the CC is a function only of force. However, it is well known that a family of F/V curves can be deduced at different levels of activation of the muscle. As the contractions performed in the present study began from a resting state of the muscle, and as activation takes time to develop, it is probable that in the early stages of isometric contraction the velocity is dependent upon both force and activation. In addition, the time to reach a given level of force is different in the two contractions (with and without the added compliance) and therefore this force will be achieved with a different level of

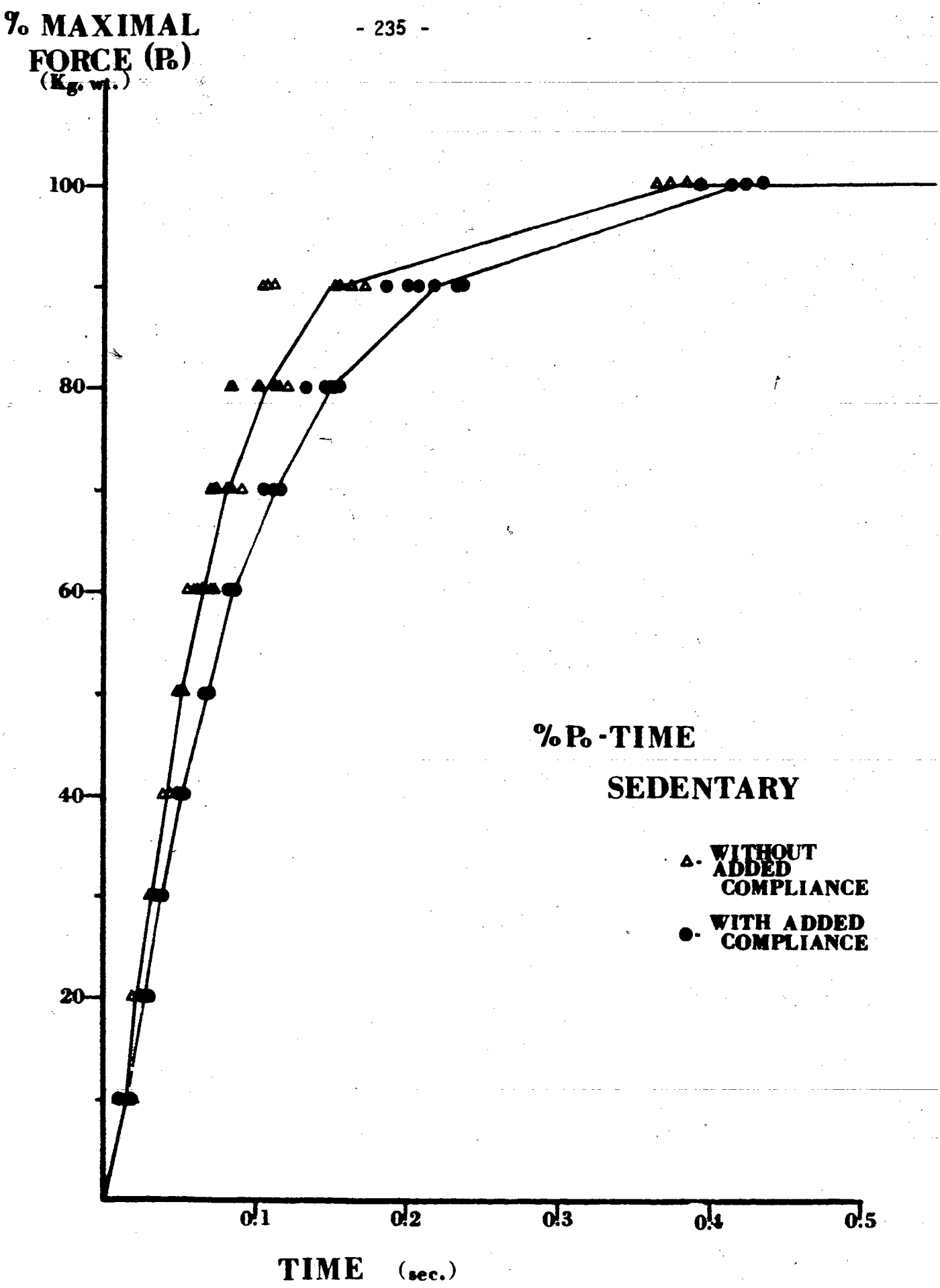
activation. Consequently the values of dP/dt will be equated with the same level of force but at different levels of activation. Thus MacPherson's assumption must be inapplicable in the early stages of isometric contractions which begin from rest, as is that part of the resulting F/V curves.

A fairly large number of isometric contractions had to be performed for each muscle to acquire two contractions with the same force. Further-more, the force decreased with the number of contractions indicating fatigue. In a number of cases, MacPherson's (1953) technique had to be applied to isometric contractions produced at different stages of fatigue. Inadvertently this would result in the incorporation of the effects of fatigue into the analysis. Therefore, it was concluded that the isometric force-time curves should be analyzed in terms of percentage maximal force (P_o) to eliminate the problems encountered with muscle fatigue and acquisition of two isometric contractions with the same eventual steady state (Figure 36). The conversion of each isometric F/T curve to $\%P_o/T$ curves therefore would present a mean value curve which discounted the effects of fatigue during the non-linear analysis and indirectly would simplify the appraisal of both types of isometric contractions by the linear technique.

Figure 36 shows the mean $\%P_o/T$ curves of two types of isometric contractions, one with and the other without an added series compliance, of a sedentary muscle. There was no significant difference between a number of contractions at equal increments of forces up to and including 60% of P_o for both types of isometric contractions. Beyond 60% of P_o, fatigue had a noticeable effect on the rates of force development and thus maximal force produced. Keeping these observations in mind, MacPherson's (1953) technique can be used. The linear model was found to be virtually unaffected by fatigue due to the fact that the analysis required time

FIGURE 36:

$\%P_o$-Time relationship of a series of isometric contractions performed by the gastrocnemius of a sedentary rat. Two types of isometric contractions are shown, (Δ) without an added compliance, and (●) with an added compliance.


% MAXIMAL FORCE (Po)
(Kg. wt.)
100
80
60
40
20
0.1
0.2
0.3
0.4
0.5
TIME (sec.)
% Po - TIME
SEDENTARY
Δ- WITHOUT ADDED COMPLIANCE
●- WITH ADDED COMPLIANCE

measurements at 63.2% of P_o.

v) Summary

The present study has shown that the mechanical behavior of the various components of Hill's (1950) model of muscle are unique to the mode of contraction. Previous investigators have demonstrated that the isometric F/V relationship of the CC was distinctly different from that produced during dynamic contractions. This observation has also been made in the present study. It was shown that the non-linear F/V relationship of the CC demonstrated a rapid rise in velocity reaching a peak level at low forces. The velocity of shortening of the CC was then observed to decrease as force increased, not unlike that seen in the data obtained from dynamic contractions. It was concluded that the rapid rise in velocity of shortening of the CC at low forces was the direct result of a rising state of activation in the muscle, internal viscosity, and the changing compliance of the cross-bridges.

The results presented by Wilkie (1950) suggested that the isometric C/F relationship of the SEC shown in the present investigation was unique to isometric contractions. The compliance of the SEC was observed to rise rapidly, from a very low level, to a peak value at low forces and then decreased as force increased during isometric force production. The sedentary and trained (sub-group 2) groups showed that the compliance of the SEC formed a plateau where the values of compliance changed very little. This plateau occured at forces between 50 and 80% of P_o. Beyond 80% P_o the compliance of the SEC was observed to decrease dramatically, resulting in increased resistance to stretch. It was suggested that this shape indicated the effects of a rising state of activation.

The isometric E/F relationship of the SEC was found to bear a strong resemblance to that produced during dynamic contractions. The only difference in shape observed was present in the early stages of force development where there were relatively small changes in length of the SEC. This portion of the isometric E/F relationship corresponded to the early rise in compliance of the SEC and thus indicated the introduction and increased involvement of the extension properties of the cross-bridges during the rising state of activation. When maximal activation of the muscle was reached, the isometric E/F relationship of the SEC was observed to resemble that produced during dynamic contractions. It was concluded that the early portion of this relationship demonstrated that the SEC was activation dependent at low forces. Furthermore, it was suggested that the isometric E/F relationship of the SEC was sigmoid in shape which was distinctly different than the exponential relationship found during dynamic contractions.

The F/L relationships of the CC and PEC of the rat gastrocnemius were found to be similar in shape to those present in the literature for muscles of other animals. The force produced by the CC of the rat gastrocnemius was observed to increase, leveling off to form a plateau where maximal contractile force was developed as L_o was approached. This plateau occurred at ML's less than L_o, where L_o was positioned at a point where contractile force just started to decrease. The force developed by the CC progressively declined for ML's greater than L_o. It was concluded that this characteristic relationship of the CC coould be explained in terms of the area of overlap of the myofilaments present in the muscle. The resting length (L_o) of the rat gastrocnemius was found to be indicated by the first changes in force as the muscle was passively stretched. When L_o was

determined, the transmission of force by the PEC was observed to increase exponentially with additional passive increases in ML while there was no indication of force transmission for ML's less than L_o. The conclusion was made that the F/L relationship of the PEC reflected the mechanical behavior to changes in ML of connective tissue on the musculo-tendinous system.

The comparison of the mechanical behavior of a linear and non-linear model of muscle produced some very interesting observations. It was shown when the individual mechanical parameters of the two models were compared, that all the linear relationships eliminated some of the essential characteristics of the non-linear relationships which were unique to isometric contractions. Although this has to be expected when applying the process of linearization, it would make it very difficult to distinguish the linear relationship produced from dynamic contractions. When the linear and non-linear relationships of all the experimental groups were compared, it was found that the linear model indicated the overall trends, demonstrated by the non-linear model, which were the result of the experimental treatments. The most important result of this comparison was the fact that the linear model consistently overestimated the mechanical behavior of the non-linear model. It was found that this overestimation was the direct result of one of the basic assumptions of the linear model. The linear model assumed that the force generator (Fm) was instantaneously activated maximally which would result in an exponential rise in isometric force with time. It was observed that during isometric force development there was a much slower rise in force just after the onset of stimulation than would be expected if this assumption was true. To accomodate this assumption it was found necessary to ignore the early

portion of the F/T curves. Hence, these curves were altered to produce a true exponential curve. This alteration was found to produce a 20% smaller value of the time taken to reach 63.2% of P_o for all the experimental groups. It was concluded that this underestimation of the time constants must be taken into account before using this linear model to analyze isometric contractions.

Prolonged denervation and training were found to affect large changes in the mechanical behavior of all the various components of the linear and non-linear models of muscle. Prolonged denervation was shown to produce progressive reductions in mean P_o and peak velocity of the F/V relationship of the CC. There was sufficient evidence to suggest that the speed of shortening of the CC suffered the greatest effects of denervation. In contrast, training produced an increase in mean peak velocity of shortening of the CC while demonstrating little effect on most of the course and mean P_o of this relationship when compared to the F/V relationship of the sedentary group. It was concluded that prolonged denervation reduced enzymatic activity and myofibrillar concentrations and thus affected the observed changes in the F/V relationship of the CC. In addition, the F/V relationship of the CC of the trained (sub-group 2) group suggested that the particular training program used in this study produced increased enzymatic activity while having little effect on myofibrillar protein concentrations.

The C/F relationship indicated similar dramatic changes in the mechanical behavior of the SEC as were observed for the CC due to the experimental treatments. Prolonged denervation was shown to affect progressive increases in mean peak compliance and rate of rise to peak compliance of the SEC while reducing the range of isometric force. These

findings were suggested to be the direct results of decreased numbers of available cross-bridges which was due to the progressive fragmentation and digestion of myofilaments during denervation. On the other hand, training was observed to increase the peak compliance of the SEC at low forces but demonstrated little effect on the majority of the C/F relationship when compared to that of the sedentary group. It was suggested that the increased compliance at low forces was the consequence of accelerated electrical or chamical activity around the cross-bridges which may have been indicative of an increase in sarcoplasmic protein concentrations and/or rate of activation of the muscle.

The E/F relationships of the SEC for all the experimental groups were sigmoid in shape. Prolonged denervation resulted in significant decreases in maximal extension and increases in the rate of length changes of the SEC when compared with the E/F relationship of the sedentary group. Conversely, training produced an increase in both these parameters. An interesting coincidence was found between the maximal velocity of shortening of the CC and the maxiamal extension of the SEC. This coincidence suggested that the extension of the SEC was velocity dependent and thus directly related to the effects of the numbers and activity of the cross-bridges on the properties of compliance of the cross-bridges themselves.

Prolonged denervation, disuse and training were shown to increase the slope and decrease the length axis intercept of the F/L relationship of the PEC. Prolonged denervation was observed to increase significantly the concentration of connective tissue within the muscle. It was concluded that the increase of connective tissue produced the stiffening effect observed in the PEC. Similar increases in connective tissue or stiffness of the existing connective tissue were suspected to have produced the

effects demonstrated by prolonged disuse and training on the PEC.

The F/L relationship of the CC indicated that denervation and training had dramatic effects on the magnitude of force development for the full range of ML's. As in the comparison of the F/V relationships of the GC, prolonged denervation resulted in significant decreases in force, while training demonstrated little effect on force production when compared to the F/L relationship of the sedentary group. These results confirmed that denervation had a significant effect on the CC resulting from fragmentation and digestion of the myofilaments. The earlier conclusion that the training program used in the present investigation had virtually no effect on force production and myofibrillar protein concentrations tends to be substantiated by these results.

CHAPTER VI

CONCLUSIONS

A number of important aspects of muscular biomechanics were investigated in this thesis.

A great deal of research has been devoted to the determination of the mechanical properties and to the development of a reasonably accurate model to depict these properties of muscle. Most of this research has been concerned with dynamic contractions. Although the mechanical behavior of the CC has been determined for isometric contractions, the mechanical properties of the SEC have not been accurately reported for isometric contractions. It was found here that the mechanical behavior of the SEC during isometric contractions was different from that produced during dynamic contractions. It has to be stated that one of the most important descriptive relationships of the mechanical properties of the SEC has been sadly overlooked. The C/F relationship during isometric contractions provides a unique insight into the mechanical behavior of the SEC. It was suggested that a rising state of activation had a significant effect on behavior of the SEC. Additional research is necessary to determine the mechanical behavior of the SEC for different levels of activation.

Denervation was found to have a significant effect on both the mechanical properties and structure of the muscle. The effects of training were not as obvious. The results of this study and many others have presented one major fact, that is that the training programs used by researchers are as numerous as the investigators. It is suggested that there must be some guidelines or limits defined to describe the various

types of training programs and their effects. No concise conclusions can be made concerning structural and/or mechanical change in muscle until these defined standards are achieved.

Houk's (1963) linear model of muscle was found to supply a fairly good representation of the non-linear mechanical properties of the CC and SEC during isometric contractions. Furthermore, the linear model indicated gross changes, demonstrated by the non-linear model, in the mechanical behavior of the CC and SEC which were the result of the experimental treatment. It is suggested that there would be some difficulty on distinguishing between the linear parameters produced during isometric and dynamic contractions. Generally the linear model provides a simple method of determining gross changes in the mechanical behavior of the CC and SEC, but if more specific information is necessary, another system of analysis and model should be considered.

MacPherson's (1953) technique was shown to be an ideal, but somewhat cumbersome method of analyzing isometric contractions once the level of activation reached maximal. By utilizing computerized data analysis and converting the F/T curves to $\%P_o/T$ curves, the greatest portion of the ponderous details would be eliminated.

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APPENDIX 1: NON-LINEAR ANALYSIS RAW DATA

LEGEND:

P	Force in grams weight
$\frac{DP}{DT}_o$	Change in force with respect to time (without added compliance) (gm.wt./sec.)
$\frac{DP}{DT}_c$	Change in force with respect to time (with added compliance) (gm.wt./sec.)
$\frac{DX_2}{DP^2}$	Compliance of added spring in cm./gm.
$\frac{DX_1}{DP}$	Compliance of SEC at any value of P (cm./gm.)
$\frac{DX_1}{DT}$	Velocity of shortening of CC at any value of P (cm./sec.)

CONDITION: DENERVATED 1 MONTH
RAT NUMBER: 1
RAT WEIGHT: 593.8 gm
MUSCLE WEIGHT: 3.0760 gm
MUSCLE LENGTH: 5.3 cm
PRETENSION: 77 gm

P	$\frac{DP}{DT}$ C	$\frac{DP}{DT}$ C	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
100	745	430	0.0001	0.000137	0.10
125	3180	2700	0.0001	0.000563	1.79
150	2880	2400	0.0001	0.000500	1.44
175	2860	2360	0.0001	0.000472	1.35
200	2170	1590	0.0001	0.000274	0.59
225	1520	1030	0.0001	0.000210	0.32
250	415	500	0.0001		
269					0.00

CONDITION: DENERVATED 1 MONTH
RAT NUMBER: 2
RAT WEIGHT: 668.7 gm
MUSCLE WEIGHT: 3.1662 gm
MUSCLE LENGTH: 5.4 cm
PRETENSION: 39 gm

P	$\frac{DP}{DT}$ C	$\frac{DP}{DT}$ C	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
50	1390	2220	0.0001	0.000267	0.37
75	4060	3040	0.0001	0.000298	1.21
100	3240	2780	0.0001	0.000604	1.96
125	2910	2530	0.0001	0.000666	1.94
150	2780	2340	0.0001	0.000532	1.48
175	2680	2220	0.0001	0.000483	1.29
200	2360	1980	0.0001	0.000521	1.23
225	1900	1220	0.0001	0.000179	0.34
250	1740	1050	0.0001	0.000152	0.26
300	512	172	0.0001	0.000051	0.03
321					0.00

CONDITION: DENERVATED 1 MONTH
RAT NUMBER: 3
RAT WEIGHT: 709.0 gm
MUSCLE WEIGHT: 2.9710 gm
MUSCLE LENGTH: 5.9 cm
PRETENSION: 18 gm

P	$\frac{DP}{DT}$ C	$\frac{DP}{DT}$ C	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
50	2700	2180	0.0001	0.000405	1.08
75	3600	3000	0.0001	0.000500	1.80
100	3830	3260	0.0001	0.000570	2.18
125	3830	2780	0.0001	0.000485	1.86
150	2880	2280	0.0001	0.000405	1.15
175	2380	1860	0.0001	0.000346	0.83
200	1770	1360	0.0001	0.000330	0.59
225	1040	790	0.0001	0.000316	0.33
250	390	200	0.0001	0.000100	0.04
252					0.00

CONDITION: DENERVATED 2 MONTHS
RAT NUMBER: 5
RAT WEIGHT: 634.1 gm.
MUSCLE WEIGHT: .4167 gm.
MUSCLE LENGTH: 5.8 cm.
PRETENSION: 54 gm.

P	$\frac{DP}{DT}$ o	$\frac{DP}{DT}$ c	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
12.5	850	675	0.0001	0.000368	0.32
25.0	780	643	0.0001	0.000470	0.37
37.5	745	588	0.0001	0.000370	0.28
50.0	705	570	0.0001	0.000422	0.30
62.5	376	250	0.0001	0.000202	0.08
83.0					0.00

CONDITION: DENERVATED 2 MONTHS
RAT NUMBER: 4
RAT WEIGHT: 617.0 gm.
MUSCLE WEIGHT: 2.2362 gm.
MUSCLE LENGTH: 5.8 cm.
PRETENSION: 50 gm.

P	$\frac{DP}{DT}$ b	$\frac{DP}{DT}$ c	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_2}{DT}$
12.5	845	658	0.0001	0.000350	0.30
25.0	730	658	0.0001	0.000805	0.59
37.5	600	530	0.0001	0.000755	0.45
50.0	415	366	0.0001	0.000748	0.33
62.5	160	138	0.0001	0.000660	0.11
85.0					0.00

CONDITION: DENERVATED 2 MONTHS (ANTERIOR MUSCLES)
RAT NUMBER: 6
RAT WEIGHT: 655.6 gm.
MUSCLE WEIGHT: 4.6913 gm.
MUSCLE LENGTH: 4.8 cm.
PRETENSION: 83 gm.

P	$\frac{DP}{DT}$ o	$\frac{DP}{DT}$ c	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
100	11800	8900	0.0001	0.000306	3.62
200	12400	9800	0.0001	0.000376	4.67
300	13900	10400	0.0001	0.000297	4.13
400	13900	10400	0.0001	0.000297	4.13
500	13900	10500	0.0001	0.000300	4.17
600	13900	9500	0.0001	0.000217	3.02
700	12300	7700	0.0001	0.000167	2.03
800	9700	6630	0.0001	0.000220	2.13
900	8190	5450	0.0001	0.000202	1.64
1000	6230	4020	0.0001	0.000182	1.13
1100	2940	1820	0.0001	0.000162	0.48
1200	1030	247	0.0001	0.000031	0.32
1300					0.00

CONDITION: SEDENTARY
RAT NUMBER: 1
RAT WEIGHT: 656.3 gm.
MUSCLE WEIGHT: 5.0391 gm.
MUSCLE LENGTH: 5.2 cm.
PRETENSION: 63 gm.

P	$\frac{DP}{DT}_o$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	10000	25000	0.0001	0.000066	1.65
400	37000	28000	0.0001	0.000311	11.51
600	35000	26300	0.0001	0.000302	10.57
800	28000	19100	0.0001	0.000215	6.02
1000	26600	17500	0.0001	0.000192	5.11
1200	22700	15400	0.0001	0.000211	4.79
1400	21000	14400	0.0001	0.000218	4.58
1600	16100	11800	0.0001	0.000274	4.41
1800	14000	8600	0.0001	0.000159	2.23
2000	10700	6200	0.0001	0.000138	1.48
2200	3700	4100	0.0001	0.000089	0.77
2400	4000	1800	0.0001	0.000082	0.33
2600	1530	690	0.0001	0.000082	0.13
2688					0.00

CONDITION: SEDENTARY
RAT NUMBER: 2
RAT WEIGHT: 765.9 gm.
MUSCLE WEIGHT: 4.9247 gm.
MUSCLE LENGTH: 5.3 cm.
PRETENSION: 80 gm.

P	$\frac{DP}{DT}_c$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	23600	15800	0.0001	0.000203	4.79
400	30000	23000	0.0001	0.000329	9.87
600	30000	22400	0.0001	0.000295	8.85
800	30000	21100	0.0001	0.000237	7.11
1000	27800	19400	0.0001	0.000231	6.42
1200	24800	17800	0.0001	0.000254	6.30
1400	22800	14500	0.0001	0.000175	3.99
1600	16700	11500	0.0001	0.000221	3.69
1800	12500	8000	0.0001	0.000178	2.23
2000	7600	4830	0.0001	0.000174	1.32
2200	3480	1430	0.0001	0.000070	0.24
2400	1040	530	0.0001	0.000104	0.11
2560					0.00

CONDITION: SEDENTARY
RAT NUMBER: 3
RAT WEIGHT: 698.3 gm.
MUSCLE WEIGHT: 4.6900 gm.
MUSCLE LENGTH: 5.2 cm.
PRETENSION: 267 gm.

P	$\frac{DP}{DT}$ o	$\frac{DP}{DT}$ c	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
400	25800	20000	0.0001	0.000345	8.90
600	27500	22900	0.0001	0.000498	13.70
800	27500	22500	0.0001	0.000450	12.38
1000	27500	20000	0.0001	0.000267	7.34
1200	27500	17100	0.0001	0.000164	4.51
1400	24400	15200	0.0001	0.000165	4.03
1600	22600	13500	0.0001	0.000148	3.35
1800	20000	12100	0.0001	0.000153	3.06
2000	18100	10500	0.0001	0.000138	2.50
2200	13300	8080	0.0001	0.000155	2.06
2400	10200	5200	0.0001	0.000104	1.06
2600	7220	2310	0.0001	0.000047	0.34
2800	2360	833	0.0001	0.000055	0.13
2867					0.00

CONDITION: SEDENTARY
RAT NUMBER: 4
RAT WEIGHT: 705.0 gm.
MUSCLE WEIGHT: 5.1427 gm.
MUSCLE LENGTH: 5.3 cm.
PRETENSION: 333 gm.

P	$\frac{DP}{DT}_o$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
400	26700	15600	0.0001	0.000141	3.77
600	36800	27700	0.0001	0.000304	11.19
800	32300	21300	0.0001	0.000213	6.88
1000	31100	20000	0.0001	0.000180	5.60
1200	30500	17600	0.0001	0.000136	4.15
1400	30000	15000	0.0001	0.000100	3.00
1600	28300	13100	0.0001	0.000086	2.43
1800	27000	11900	0.0001	0.000079	2.13
2000	25100	11900	0.0001	0.000090	2.26
2200	19000	9000	0.0001	0.000090	1.71
2400	17300	8350	0.0001	0.000093	1.61
2600	11300	5840	0.0001	0.000107	1.21
2800	7810	3880	0.0001	0.000099	0.77
3000	2800	1240	0.0001	0.000079	0.22
3267					0.00

CONDITION: SEDENTARY
RAT NUMBER: 5
RAT WEIGHT: 612.4 gm.
MUSCLE WEIGHT: 4.8291 gm.
MUSCLE LENGTH: 5.3 cm.
PRETENSION: 111 gm.

P	$\frac{DP}{DT}_o$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DI}$
200	18700	14200	0.0001	0.000316	5.91
400	27200	21300	0.0001	0.000361	9.82
600	30200	24100	0.0001	0.000395	11.93
800	32300	25000	0.0001	0.000342	11.05
1000	34900	25900	0.0001	0.000288	10.05
1200	34900	25900	0.0001	0.000288	10.05
1400	32700	23800	0.0001	0.000267	8.73
1600	29100	19400	0.0001	0.000200	5.82
1800	25800	17200	0.0001	0.000200	5.16
2000	22800	14700	0.0001	0.000181	4.13
2200	18100	11300	0.0001	0.000166	3.00
2400	13900	8690	0.0001	0.000167	2.32
2600	9730	5480	0.0001	0.000129	1.26
2800	9730	1820	0.0001	0.000089	0.34
2822					0.00

CONDITION: TRAINED (SICK)
RAT NUMBER: 1
RAT WEIGHT: 774.8 gm.
MUSCLE WEIGHT: 5.6387 gm.
MUSCLE LENGTH: 5.2 cm.
PRETENSION: 150 gm.

P	$\frac{DP}{DT}_a$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	7400	6050	0.0001	0.000448	3.32
400	11950	10900	0.0001	0.001038	12.40
600	12000	10900	0.0001	0.000991	11.89
800	12000	10000	0.0001	0.000500	6.00
1000	12000	8180	0.0001	0.000214	2.57
1200	9800	6720	0.0001	0.000218	2.14
1400	8900	6330	0.0001	0.000246	2.19
1600	6360	4100	0.0001	0.000181	1.15
1800	4210	2600	0.0001	0.000161	0.68
1950					0.00

CONDITION: TRAINED (SICK)
RAT NUMBER: 2
RAT WEIGHT: 579.9 gm.
MUSCLE WEIGHT: 5.4672 gm.
MUSCLE LENGTH: 5.2 cm.
PRETENSION: 75 gm.

P	$\frac{DP}{DT}_a$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	13700	10700	0.0001	0.000357	4.88
400	18300	14500	0.0001	0.000382	6.99
600	16300	12500	0.0001	0.000329	5.36
800	14000	10900	0.0001	0.000352	4.93
1000	11400	8500	0.0001	0.000304	3.47
1200	8400	6300	0.0001	0.000300	2.52
1400	5500	3200	0.0001	0.000139	0.76
1600	1800	1100	0.0001	0.000122	0.22
1790					0.00

CONDITION: TRAINED
RAT NUMBER: 3
RAT WEIGHT: 678.1 gm.
MUSCLE WEIGHT: 5.6544 gm.
MUSCLE LENGTH: 5.3 cm.
PRETENSION: 80 gm.

P	$\frac{DP}{DT}_o$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	17600	13300	0.0001	0.000309	5.44
400	23700	20900	0.0001	0.000746	17.68
600	21500	18100	0.0001	0.000532	11.44
800	21500	17600	0.0001	0.000451	9.70
1000	21500	16400	0.0001	0.000322	6.92
1200	21500	15200	0.0001	0.000241	5.18
1400	21200	14300	0.0001	0.000207	4.39
1600	18100	11800	0.0001	0.000187	3.38
1800	11200	8000	0.0001	0.000250	2.80
2000	5330	3900	0.0001	0.000273	1.46
2200	2000	857	0.0001	0.000075	0.15
2320					0.00

CONDITION: TRAINED
RAT NUMBER: 4
RAT WEIGHT: 662.6 gm.
MUSCLE WEIGHT: 5.8803 gm.
MUSCLE LENGTH: 5.2 cm.
PRETENSION: 0 gm.

P	$\frac{DP}{DT}_o$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	23300	18500	0.0001	0.000385	8.97
400	26600	23500	0.0001	0.000758	20.16
600	30600	22400	0.0001	0.000273	8.35
800	27900	27800	0.0001	0.000176	4.91
1000	27600	27500	0.0001	0.000173	4.77
1200	27100	16800	0.0001	0.000163	4.42
1400	25200	15600	0.0001	0.000163	4.11
1600	20700	13300	0.0001	0.000180	3.73
1800	19100	10500	0.0001	0.000122	2.33
2000	14500	8600	0.0001	0.000146	2.12
2200	11700	6200	0.0001	0.000113	1.32
2400	6940	3580	0.0001	0.000107	0.74
2600	4260	1970	0.0001	0.000096	0.37
2800	1570	443	0.0001	0.000039	0.06
2867					0.00

CONDITION: TRAINED
RAT NUMBER: 5
RAT WEIGHT: 700.0 gm.
MUSCLE WEIGHT: 5.6790 gm.
MUSCLE LENGTH: 5.3 cm.
PRETENSION: 333 gm.

P	$\frac{DP}{DT}_o$	$\frac{DP}{DT}_c$	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
400	16200	12900	0.0001	0.000391	6.33
600	24300	21300	0.0001	0.000710	17.25
800	29100	20900	0.0001	0.000252	7.33
1000	29100	18900	0.0001	0.000185	5.38
1200	29100	17900	0.0001	0.000160	4.66
1400	23500	15700	0.0001	0.000201	4.72
1600	18600	12300	0.0001	0.000195	3.63
1800	17800	11500	0.0001	0.000183	3.26
2000	13900	9500	0.0001	0.000216	3.00
2200	12000	8040	0.0001	0.000203	2.44
2400	8340	5520	0.0001	0.000196	1.63
2600	4380	2340	0.0001	0.000115	0.50
2733					0.00

CONDITION: TRAINED
RAT NUMBER: 6
RAT WEIGHT: 683.7 gm.
MUSCLE WEIGHT: 5.5158 gm.
MUSCLE LENGTH: 5.1 cm.
PRETENSION: 133 gm.

P	$\frac{DP}{DT}$ o	$\frac{DP}{DT}$ c	$\frac{DX_2}{DP}$	$\frac{DX_1}{DP}$	$\frac{DX_1}{DT}$
200	22600	18300	0.0001	0.000426	9.63
400	30000	25700	0.0001	0.000589	17.94
600	30000	23300	0.0001	0.000348	10.44
800	30200	21000	0.0001	0.000228	6.89
1000	30200	19500	0.0001	0.000182	5.50
1200	30200	16500	0.0001	0.000120	3.62
1400	25900	14500	0.0001	0.000127	3.29
1600	32200	12400	0.0001	0.000115	2.67
1800	20900	10800	0.0001	0.000107	2.24
2000	15600	9210	0.0001	0.000144	2.25
2200	11300	6740	0.0001	0.000148	1.67
2400	9170	4660	0.0001	0.000103	0.95
2600	6790	2670	0.0001	0.000065	0.44
2800	1390	500	0.0001	0.000056	0.08
2867					0.00

APPENDIX 2: LINEAR ANALYSIS RAW DATA SHEETS

LEGEND:

WO	Without added compliance
W	With added compliance
*	Data used for the non-linear analysis
max.	Maximal force produced in divisions
min.	Force level in divisions where contractions were initiated
γ	Time (sec.) taken to reach 63% of maximal force

CONDITION: DENERVATED 1 MONTH
RAT NUMBER: 1
RAT WEIGHT: 593.8 gm.
MUSCLE WEIGHT: 3.0760 gm.
MUSCLE LENGTH: 5.3 cm.

RUN	CONDITION	MAX.	MIN.	T
1	W	19.8	8.75	0.055
2*	W	20.0	8.00	0.055
3	WO	19.0	8.50	0.045
4*	WO	20.0	8.25	0.040
5	W	15.0	6.50	0.055
6	W	15.5	6.25	0.055
7	W	17.0	6.25	0.058
8	W	16.5	6.25	0.050
9	WO	22.0	5.00	0.045
10	WO	22.5	5.00	0.040
11	W	20.0	0.25	0.058
12	W	19.0	0.50	0.055

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0
100	10
200	20.5
300	31
400	41.5
500	52

CONDITION: DENERVATED 1 MONTH
RAT NUMBER: 2
RAT WEIGHT: 668.7 gm.
MUSCLE WEIGHT: 3.1662 gm.
MUSCLE LENGTH: 5.4 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	42.3	2.75	0.070
2	WO	42.8	1.00	0.058
3	W	37.0	5.25	0.068
4	W	38.0	5.25	0.068
5	W	39.0	10.0	0.068
6	W	39.8	9.00	0.065
7	WO	39.5	5.50	0.058
8*	WO	39.5	5.50	0.058
9	W	39.0	6.50	0.063
10	W	38.5	6.25	0.060
11*	W	39.5	6.25	0.050
12	WO	36.0	5.25	0.055
13	WO	36.0	5.00	0.050
14	WO	35.0	5.00	0.050
15	WO	35.5	5.50	0.050
16	WO	35.3	5.50	0.050
17	WO	37.0	5.50	0.055
18	WO	37.5	6.00	0.048
19	WO	36.5	6.00	0.048
20	WO	37.0	6.00	0.050

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0
100	14
200	28
300	42
400	56
500	70

CONDITION: DENERVATED 1 MONTH
RAT NUMBER: 3
RAT WEIGHT: 709.0 gm.
MUSCLE WEIGHT: 2.9710 gm.
MUSCLE LENGTH: 5.9 cm.

RUN	CONDITION	MAX.	MIN.	/
1	WO	51.3	2.75	0.050
2	WO	51.3	2.50	0.050
3	WO	53.0	2.25	0.048
4	W	52.0	2.75	0.058
5*	W	36.0	2.75	0.058
6	W	34.8	3.00	0.058
7	WO	32.5	2.00	0.048
8	WO	31.5	2.00	0.048
9*	WO	36.0	3.00	0.050
10	WO	34.0	2.75	0.050

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0
100	11
200	28
300	44
400	61
500	77

CONDITION: DENERVATED 2 MONTHS
RAT NUMBER: 4
RAT WEIGHT: 617.0 gm.
MUSCLE WEIGHT: 2.2362 gm.
MUSCLE LENGTH: 5.8 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	8.00	1.00	0.043
2	WO	8.50	1.25	0.045
3	W	2.00	1.60	0.050
4	W	2.00	1.75	0.055
5	W	2.00	1.75	0.050
6	W	3.25	2.25	0.070
7	W	3.00	2.25	0.060
8*	W	4.50	3.00	0.055
9	W	4.00	3.00	0.055
10	W	4.00	6.00	0.055
11	WO	5.00	3.25	0.058
12	WO	4.50	3.25	0.045
13	WO	4.50	3.00	0.045
14	WO	5.00	3.00	0.045
15*	WO	4.50	3.00	0.045
16	W	2.00	3.50	0.055
17	W	2.00	3.25	0.065
18	W	2.00	8.75	0.055
19	W	3.50	3.50	0.055
20	WO	4.00	3.25	0.048

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0
100	6
200	12
300	18
400	24
500	30

CONDITION: DENERVATED 2 MONTHS
RAT NUMBER: 5
RAT WEIGHT: 634.1 gm.
MUSCLE WEIGHT: 2.4167 gm.
MUSCLE LENGTH: 5.8 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	7.25	2.00	0.035
2	WO	7.50	1.75	0.040
3	W	4.50	4.50	0.053
4	W	4.25	4.25	0.050
5	W	4.00	4.00	0.048
6	WO	3.50	2.00	0.045
7	WO	3.50	2.00	0.045
8	WO	3.50	2.00	0.045
9*	WO	4.75	3.25	0.040
10	WO	4.50	3.25	0.043
11*	W	4.75	3.25	0.050
12	W	4.50	3.00	0.053
13	W	4.50	3.00	0.050
14	W	5.00	2.75	0.053
15	W	4.50	2.75	0.050
16	WO	4.25	3.50	0.043
17	WO	4.00	3.50	0.043
18	WO	4.00	3.50	0.043

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0
100	6
200	12
300	18
400	24
500	30

CONDITION: DENERVATED 2 MONTHS (ANTERIOR MUSCLES)
RAT NUMBER: 6
RAT WEIGHT: 655.6 gm.
MUSCLE WEIGHT: 4.6913 gm.
MUSCLE LENGTH: 4.8 cm.

RUN	CONDITION	MAX.	MIN.	
2*	W	37.5	2.50	0.070
3	W	35.5	2.50	0.070
4	W	35.5	1.50	0.070
5	WO	38.5	1.00	0.050
6	WO	38.0	1.75	0.050
7	WO	37.0	2.25	0.053
8*	WO	37.5	2.75	0.050

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0
100	3
200	6
300	9
400	12
500	15

CONDITION: SEDENTARY
RAT NUMBER: 1
RAT WEIGHT: 656.3 gm.
MUSCLE WEIGHT: 5.0391 gm.
MUSCLE LENGTH: 5.2 cm.

RUN	CONDITION	MAX.	MIN.	T
4	W	62.5	1.50	0.085
5	W	61.5	2.50	0.086
6	WO	58.0	2.00	0.065
7	WO	60.0	2.00	0.065
8	W	61.5	2.00	0.098
9	W	62.5	2.75	0.095
10	WO	71.0	2.00	0.060
11	WO	71.3	1.75	0.060
12	W	68.0	1.25	0.090
13	W	68.0	2.00	0.090
14	WO	71.0	1.00	0.065
15	WO	72.0	1.00	0.065
16	W	63.0	1.75	0.090
17*	W	64.5	2.50	0.090
18*	WO	64.5	1.50	0.063
19	WO	67.0	1.25	0.065
20	W	54.0	2.00	0.090
21	W	57.0	2.50	0.095

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0.0
100	2.0
200	4.5
300	7.0
400	9.5
500	12.5

CONDITION: SEDENTARY
RAT NUMBER: 2
RAT WEIGHT: 765.9 gm.
MUSCLE WEIGHT: 4.9247 gm.
MUSCLE LENGTH: 5.3 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	33.3	1.25	0.050
2	WO	33.5	1.25	0.058
3	WO	33.5	1.00	0.053
4*	W	31.0	1.00	0.078
5	W	29.0	1.00	0.083
6	W	28.3	0.75	0.080
7	WO	32.0	1.00	0.060
8	WO	31.0	1.25	0.060
9*	WO	31.0	1.25	0.060
10	W	26.0	1.00	0.095
11	W	24.0	1.25	0.085
12	W	24.5	1.50	0.090
13	W	25.5	1.25	0.083
14	WO	26.8	0.50	0.070
15	WO	26.0	0.50	0.065
16	WO	25.5	0.50	0.068
17	WO	24.5	0.50	0.068

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0.00
100	1.25
200	2.50
300	3.75
400	5.00
500	6.25

CONDITION: SEDENTARY
RAT NUMBER: 3
RAT WEIGHT: 698.3 gm.
MUSCLE WEIGHT: 4.6900 gm.
MUSCLE LENGTH: 5.2 cm.

RUN	CONDITION	MAX.	MIN.	
1*	WO	19.5	2.00	0.060
2	WO	20.3	1.75	0.060
3	WO	21.3	1.75	0.053
4	W	19.0	2.25	0.080
5	W	18.8	2.25	0.083
6	W	17.8	2.25	0.082
7	WO	20.8	2.25	0.055
8	WO	20.3	2.25	0.058
9	WO	20.0	2.25	0.063
10	W	20.8	2.25	0.090
11*	W	19.5	2.50	0.080
12	W	19.5	2.50	0.080
13	W	19.5	2.50	0.090
14	WO	22.0	2.00	0.065
15	WO	22.0	2.00	0.065
16	WO	21.5	2.00	0.063

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0.00
100	0.75
200	1.50
300	2.25
400	3.00
500	3.75

CONDITION: SEDENTARY
RAT NUMBER: 4
RAT WEIGHT: 705.0 gm.
MUSCLE WEIGHT: 5.1427 gm.
MSUCLE LENGTH: 5.3 cm.

RUN	CONDITION	MAX.	MIN.	$\dot{l}$
1	WO	19.5	2.50	0.055
2	WO	20.5	2.50	0.055
3*	WO	22.0	2.50	0.053
4	W	22.5	3.00	0.080
5*	W	22.0	3.00	0.080
6	W	22.0	3.00	0.078
7	W	21.5	3.00	0.075
8	WO	23.5	3.00	0.058
9	WO	23.5	3.00	0.050
10	WO	23.0	3.00	0.055
11	WO	23.0	3.00	0.055
12	WO	23.0	3.00	0.055
13	W	20.0	3.00	0.090
14	W	19.0	3.00	0.080
15	W	19.5	3.00	0.080
16	WO	20.0	3.00	0.060
17	WO	20.5	3.00	0.060
18	WO	19.0	3.25	0.058
19	WO	19.0	3.25	0.058

CALIBRATION FIGURES

GRAMS	DIVISIONS
0	0.00
100	0.75
200	1.50
300	2.25
400	3.00
500	3.75

CONDITION: SEDENTARY
RAT NUMBER: 5
RAT WEIGHT: 612.4 gm.
MUSCLE WEIGHT: 4.8281 gm.
MSUCLE LENGTH: 5.3 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	62.5	2.00	0.055
2	WO	64.5	2.50	0.055
3*	WO	63.5	2.50	0.055
4*	W	63.5	2.75	0.075
5	W	62.0	3.00	0.080
6	W	61.5	3.00	0.078
7	WO	65.5	1.00	0.060
8	WO	65.0	1.00	0.058
9	WO	65.0	1.00	0.060
10	W	55.0	4.00	0.080
11	W	53.5	3.75	0.085
12	W	51.5	3.50	0.080
13	W	48.5	6.50	0.080
14	W	48.0	7.00	0.080
15	WO	49.0	5.25	0.060
16	WO	50.5	5.00	0.053
17	WO	50.0	5.00	0.055
18	WO	53.3	4.75	0.055

CALIBRATION FIGURES

GRAMS	DIVISIONS
0	0.00
100	2.25
200	4.50
300	6.75
400	9.00
500	11.25

CONDITION: TRAINED (SICK)
RAT NUMBER: 1
RAT WEIGHT: 774.8 gm.
MUSCLE WEIGHT: 5.6387 gm.
MUSCLE LENGTH: 5.2 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	36.5	3.50	0.090
2	WO	37.0	3.25	0.095
3*	WO	36.0	3.00	0.095
4*	W	36.0	3.25	0.135
5	W	35.5	3.00	0.130
6	W	35.3	2.75	0.130
7	W	33.0	6.50	0.145
8	W	32.5	6.50	0.133
9	WO	37.5	3.50	0.100
10	WO	37.5	3.50	0.100
11	WO	36.0	5.00	0.100
12	WO	34.3	4.75	0.100
13	W	22.0	4.50	0.120
14	W	20.0	5.00	0.110
15	W	18.5	6.00	0.110
16	W	22.0	3.25	0.110
17	WO	28.5	3.00	0.088
18	WO	27.0	3.00	0.088
19	WO	26.0	3.00	0.083
20	WO	24.5	3.00	0.080
21	W	24.3	2.75	0.103
22	W	22.5	2.50	0.100
23	W	21.3	2.50	0.100
24	W	21.5	3.25	0.100
25	WO	42.5	2.00	0.083
26	WO	40.5	2.00	0.080

CALIBRATION FIGURES

GRAMS	DIVISIONS
0	0.0
100	2.0
200	4.0
300	6.0
400	8.0
500	10.0

CONDITION: TRAINED (SICK)
RAT NUMBER: 2
RAT WEIGHT: 579.9 gm.
MUSCLE WEIGHT: 5.4672 gm.
MUSCLE LENGTH: 5.2 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	55.0	2.00	0.080
2	WO	54.0	1.75	0.080
3	WO	54.5	2.50	0.088
4	W	27.0	2.50	0.100
5	W	27.0	5.00	0.108
6	W	27.3	6.00	0.100
7	WO	43.5	4.00	0.075
8	WO	44.0	4.00	0.078
9	WO	43.0	4.00	0.078
10	W	27.0	5.50	0.105
11	W	26.3	10.00	0.098
12	W	25.3	12.00	0.103
13	W	28.3	6.00	0.110
14	W	25.0	8.50	0.110
15	W	32.5	1.50	0.105
16*	W	34.3	1.75	0.098
17	WO	30.3	1.25	0.075
18	WO	33.0	2.00	0.065
19*	WO	34.3	1.50	0.060
20	W	25.8	1.50	0.093
21	W	24.5	1.75	0.100
22	W	28.5	1.75	0.095
23	W	27.5	2.00	0.090

CALIBRATION FIGURES

GRAMS	DIVISIONS
0	0.0
100	2.0
200	4.0
300	6.0
400	8.0
500	10.0

CONDITION: TRAINED
RAT NUMBER: 3
RAT WEIGHT: 678.1 gm.
MUSCLE WEIGHT: 5.6544 gm.
MUSCLE LENGTH: 5.3 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	20.0	1.00	0.060
2	WO	21.0	1.00	0.060
3	W	21.5	1.50	0.100
4	W	18.8	1.50	0.080
5	W	18.5	1.50	0.085
6	WO	21.5	1.00	0.070
7	WO	20.8	1.25	0.070
8*	W	28.0	1.25	0.083
9	W	26.8	1.25	0.083
10	W	26.3	1.25	0.080
11	WO	30.0	1.00	0.060
12	WO	29.0	1.00	0.060
13*	WO	28.0	1.00	0.060
14	W	22.0	1.00	0.075
15	W	21.0	1.00	0.075
16	W	21.8	1.25	0.075
17	W	20.3	1.75	0.078
18	W	20.0	1.75	0.075
19	W	19.3	1.75	0.075

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0.00
100	1.25
200	2.50
300	3.75
400	5.00
500	6.25

CONDITION: TRAINED
RAT NUMBER: 4
RAT WEIGHT: 662.6 gm.
MUSCLE WEIGHT: 5.8803 gm.
MUSCLE LENGTH: 5.2 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	47.5	1.50	0.060
2	WO	49.8	1.25	0.065
3	W	21.0	0.00	0.100
4*	W	21.5	0.00	0.100
5	WO	22.5	2.50	0.075
6*	WO	21.5	2.50	0.075
7	WO	21.8	2.25	0.073
8	W	18.0	3.00	0.098
9	W	17.5	3.00	0.098
10	W	16.8	3.00	0.095
11	W	17.0	2.00	0.090
12	WO	18.8	2.00	0.075
13	WO	18.0	2.00	0.073
14	WO	17.5	2.00	0.075
15	WO	16.5	2.00	0.075
16	W	11.5	2.25	0.090
17	W	10.0	2.25	0.090

CALIBRATION FIGURES:

GRAMS	BIVISIONS
0	0.00
100	0.75
200	1.50
300	2.25
400	3.00
500	3.75

CONDITION: TRAINED
RAT NUMBER: 5
RAT WEIGHT: 700.00 gm.
MUSCLE WEIGHT: 5.6790 gm.
MUSCLE LENGTH: 5.3 cm.

RUN	CONDITION	MAX.	MIN.	
1	WO	21.0	2.00	0.055
2	WO	21.0	2.00	0.058
3	WO	20.5	2.00	0.053
4*	W	18.0	3.00	0.080
5	W	17.0	3.00	0.080
6	W	16.8	2.75	0.080
7	W	17.3	2.75	0.080
8*	WO	18.0	2.50	0.060
9	WO	17.5	2.50	0.060
10	WO	16.5	2.50	0.060
11	WO	15.5	2.50	0.060
12	W	14.5	3.00	0.070
13	W	13.0	3.00	0.075
14	W	12.5	3.00	0.078

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0.00
100	0.75
200	1.50
300	2.25
400	3.00
500	3.75

CONDITION: TRAINED
RAT NUMBER: 6
RAT WEIGHT: 683.7 gm.
MUSCLE WEIGHT: 5.5158 gm.
MUSCLE LENGTH: 5.1 cm.

RUN	CONDITION	MAX.	MIN.	
1*	W	20.5	1.25	0.093
2	W	19.3	1.00	0.085
3	W	18.5	1.00	0.085
4	W	18.0	1.00	0.088
5*	WO	20.5	1.00	0.060
6	WO	19.5	1.00	0.063
7	WO	19.0	1.00	0.068
8	WO	18.0	1.00	0.068
9	W	15.0	3.00	0.080
10	W	14.3	3.00	0.080
11	W	14.0	2.00	0.080
12	W	13.3	2.00	0.080
13	WO	14.0	2.00	0.063
14	WO	13.5	2.00	0.063
15	WO	12.8	2.00	0.065

CALIBRATION FIGURES:

GRAMS	DIVISIONS
0	0.00
100	0.75
200	1.50
300	2.25
400	3.00
500	3.75

APPENDIX 3: FORCE-LENGTH RAW DATA SHEETS

CONDITION: DENERVATED (1 MONTH)
RAT NUMBER: 1
RAT WEIGHT: 602.4 gm.
MUSCLE WEIGHT: 2.6546 gm.
MUSCLE LENGTH: 5.8 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	7.50	500	7.50	500
-2.7	0.00	0	8.00	530	8.00	530
-2.1	0.00	0	8.00	530	8.00	530
-1.4	0.00	0	8.00	530	8.00	530
-0.7	0.00	0	7.80	520	7.80	520
0.0	0.30	20	7.30	480	7.50	500
0.7	0.50	30	6.80	450	7.30	480
1.4	0.80	50	6.70	450	7.50	500
2.1	3.00	200	5.50	370	8.50	570
2.8	6.50	430	4.00	270	10.50	700
3.5	9.50	630	3.00	200	12.50	830
4.2	9.50	630	2.50	170	12.00	800
4.9	10.00	670	2.00	130	12.00	800
5.6	17.50	1170	1.00	60	18.50	1230
6.3	24.50	1630	0.50	40	25.00	1670
7.0	29.50	1970	0.30	20	29.80	1990

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
1.5	100
3.0	200
4.5	300
6.0	400
7.5	500

CONDITION: DENERVATED (2MONTHS)
RAT NUMBER: 2
RAT WEIGHT: 544.3 gm.
MUSCLE WEIGHT: 2.4074 gm.
MUSCLE LENGTH: 5.8 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	4.50	90	4.50	90
-2.8	0.00	0	5.00	100	5.00	100
-2.1	0.00	0	5.80	116	5.80	116
-1.4	0.00	0	5.00	100	5.00	100
-0.7	0.00	0	5.50	110	5.50	110
0.0	0.30	6	4.00	80	4.30	86
0.7	2.00	40	3.80	76	5.80	116
1.4	5.50	110	2.00	40	7.50	150
2.1	15.00	300	1.80	36	16.80	336
2.8	31.00	620	1.00	20	32.00	640
3.5	53.00	1060	0.00	0	53.00	1060
4.2	60.00	1200	0.00	0	60.00	1200
4.9	62.00	1240	0.00	0	62.00	1240
5.6	70.50	1410	0.00	0	70.50	1410

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0	0
5	100
10	200
15	300
20	400
25	500

CONDITION: DENERVATED (2 MONTHS)
RAT NUMBER: 3
RAT WEIGHT: 585.3 gm.
MUSCLE WEIGHT: 1.9340 gm.
MUSCLE LENGTH: 5.7 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	6.30	126	6.30	126
-2.8	0.00	0	8.00	160	8.00	160
-2.1	0.00	0	7.50	150	7.50	150
-1.4	0.00	0	8.00	160	8.00	160
-0.7	0.00	0	8.00	160	8.00	160
0.0	0.50	10	6.50	130	7.00	140
0.7	2.30	46	5.50	110	7.80	156
1.4	6.00	120	3.80	76	9.80	196
2.1	14.00	280	2.50	50	16.50	330
2.8	27.50	550	1.50	30	29.00	580
3.5	49.00	980	1.00	20	50.00	1000
4.2	54.00	1080	0.00	0	54.00	1080
4.9	57.00	1140	0.00	0	57.00	1140
5.6	79.00	1580	0.00	0	79.00	1580

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0	0
5	100
10	200
15	300
20	400
25	500

CONDITION: SEDENTARY (GROUP 1)
RAT NUMBER: 1
RAT WEIGHT: 521.0 gm.
MUSCLE WEIGHT: 4.9963 gm.
MUSCLE LENGTH: 5.2 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	27.00	1350	27.00	1350
-2.8	0.00	0	32.50	1630	32.50	1630
-2.1	0.00	0	36.00	1800	36.00	1800
-1.4	0.00	0	39.00	1950	39.00	1950
-0.7	0.00	0	39.00	1950	39.00	1950
0.0	0.30	10	40.70	2040	41.00	2050
0.7	0.50	30	40.00	2000	40.50	2030
1.4	0.70	30	37.30	1870	38.00	1900
2.1	1.00	50	36.00	1800	37.00	1850
2.8	1.50	80	34.00	1700	35.50	1780
3.5	3.00	150	30.00	1500	33.00	1650
4.2	5.30	260	25.20	1270	30.50	1530
4.9	9.80	490	18.20	910	28.00	1400
5.6	14.00	700	14.50	730	28.50	1430
6.3	21.50	1080	8.00	400	29.50	1480
7.0	29.50	1480	3.00	350	36.50	1830
7.7	39.50	1980	2.00	100	41.50	2080
8.4	42.00	2100	1.00	50	43.00	2150

CLAIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
2.0	100
4.0	200
6.0	300
8.0	400
10.0	500

CONDITION: SEDENTARY (GROUP 1)
RAT NUMBER: 2
RAT WEIGHT: 547.1 gm.
MUSCLE WEIGHT: 5.0602 gm.
MUSCLE LENGTH: 5.2 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	29.00	1450	29.00	1450
-2.8	0.00	0	29.00	1450	29.00	1450
-2.1	0.00	0	29.50	1480	29.50	1480
-1.4	0.00	0	35.00	1750	35.00	1750
-0.7	0.00	0	33.50	1680	33.50	1680
0.0	0.50	30	32.50	1620	33.00	1650
0.7	0.50	30	32.00	1600	32.50	1630
1.4	0.80	40	30.70	1540	31.50	1580
2.1	1.30	60	28.20	1420	29.50	1480
2.8	2.50	130	25.50	1270	28.00	1400
3.5	3.50	180	22.50	1120	26.00	1300
4.2	8.00	300	20.00	1100	28.00	1400
4.9	9.50	480	16.00	800	25.50	1280
5.6	12.50	630	15.50	770	28.00	1400
6.3	17.50	880	14.00	600	31.50	1580
7.0	27.00	1350	6.50	330	33.50	1680
7.7	34.00	1700	2.50	130	36.50	1830
8.4	43.50	2180	1.50	70	45.00	2250

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
2.0	100
4.0	200
6.0	300
8.0	400
10.0	500

CONDITION: SEDENTARY (GROUP 2)
RAT NUMBER: 3
RAT WEIGHT: 583.6 gm.
MUSCLE WEIGHT: 5.1333 gm.
MUSCLE LENGTH: 5.2 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	37.00	1850	37.00	1850
-2.8	0.00	0	37.50	1880	37.50	1880
-2.1	0.00	0	37.80	1890	37.80	1890
-1.4	0.00	0	42.50	2130	42.50	2130
-0.7	0.00	0	41.00	2030	41.00	2050
0.0	0.30	10	41.70	2090	42.00	2100
0.7	2.50	130	39.80	1990	42.30	2120
1.4	5.00	250	30.00	1500	35.00	1750
2.1	7.50	380	25.00	1250	32.50	1650
2.8	10.00	500	21.30	1060	31.30	1560
3.5	15.00	750	17.50	880	32.50	1630
4.2	18.50	930	16.30	810	34.80	1740
4.9	32.50	1630	10.00	500	42.50	2130
5.6	45.50	2280	5.00	250	50.50	2530

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
2.0	100
4.0	200
6.0	300
8.0	400
10.0	500

CONDITION: SEDENTARY (GROUP 2)
RAT NUMBER: 4
RAT WEIGHT: 597.7 gm.
MUSCLE WEIGHT: 4.8407 gm.
MUSCLE LENGTH: 5.2 cm.

LENGTH	PASSIVE FORCE		ACTIVE FORCE		TOTAL FORCE	
-3.5	0.00	0	42.00	2100	42.00	2100
-2.8	0.00	0	43.50	2180	43.50	2180
-2.1	0.00	0	46.00	2300	46.00	2300
-1.4	0.00	0	47.50	2380	47.50	2380
-0.7	0.00	0	45.00	2250	45.00	2250
0.0	0.50	30	46.00	2300	46.50	2330
0.7	2.00	100	41.50	2080	43.50	2180
1.4	4.50	230	36.50	1820	41.00	2050
2.1	7.00	350	32.00	1600	39.00	1950
2.8	9.50	480	27.50	1370	37.00	1850
3.5	16.00	800	25.00	1250	41.00	2050
4.2	19.50	980	20.00	1000	39.50	1980
4.9	34.00	1700	11.00	550	45.00	2250
5.6	46.50	2330	9.00	450	55.50	2780
6.3	52.00	2600	3.50	180	55.50	2780

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
2.0	100
4.0	200
6.0	300
8.0	400
10.0	500

CONDITION: TRAINED
RAT NUMBER: 1
RAT WEIGHT: 579.5 gm.
MUSCLE WEIGHT: 5.2530 gm.
MUSCLE LENGTH: 5.2 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	31.50	2100	31.50	2100
-2.8	0.00	0	32.50	2170	32.50	2170
-2.1	0.00	0	33.00	2200	33.00	2200
-1.4	0.00	0	35.00	2330	35.00	2330
-0.7	0.00	0	34.00	2270	34.00	2270
0.0	0.50	30	31.00	2070	31.50	2100
0.7	0.60	40	29.90	1990	30.50	2030
1.4	1.00	70	28.50	1900	29.50	1970
2.1	2.00	130	25.50	1700	27.50	1830
2.8	4.30	300	18.70	1230	23.00	1530
3.5	5.50	370	15.00	1000	20.50	1370
4.2	9.00	600	10.50	700	19.50	1300
4.9	15.00	1000	7.00	470	22.00	1470
5.6	28.00	1870	2.50	160	30.50	2030
6.3	32.50	2170	1.00	60	33.50	2230
7.0	38.00	2530	0.50	40	38.50	2570

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
1.5	100
3.0	200
4.5	300
6.0	400
7.5	500

CONDITION: TRAINED
RAT NUMBER: 2
RAT WEIGHT: 563.9 gm.
MUSCLE WEIGHT: 4.8271 gm.
MUSCLE LENGTH: 5.1 cm.

LENGTH (mm)	PASSIVE (DIV)	FORCE (gm)	ACTIVE (DIV)	FORCE (gm)	TOTAL (DIV)	FORCE (gm)
-3.5	0.00	0	30.00	2000	30.00	2000
-2.8	0.00	0	34.50	2300	34.50	2300
-2.1	0.00	0	36.00	2400	36.00	2400
-1.4	0.00	0	35.50	2370	35.50	2370
-0.7	0.00	0	35.00	2330	35.00	2330
0.0	0.50	30	32.50	2170	33.00	2200
0.7	0.80	50	29.20	1950	30.00	2000
1.4	1.50	100	25.00	1670	26.50	1770
2.1	3.50	230	20.50	1370	24.00	1600
2.8	6.00	400	16.00	1070	22.00	1470
3.5	11.00	730	11.50	770	22.50	1500
4.2	17.30	1150	7.70	520	25.00	1670
4.9	26.50	1770	4.30	280	30.80	2050
5.6	33.50	2230	1.50	100	35.00	2330
6.3	38.50	2570	1.00	60	39.50	2630

CALIBRATION FIGURES:

DIVISIONS	GRAMS
0.0	0
1.5	100
3.0	200
4.5	300
6.0	400
7.5	500

APPENDIX 4: MEANS AND STANDARD DEVIATIONS OF VELOCITY CORRESPONDING TO THE LEVELS OF FORCE PRODUCED DURING ISOMETRIC CONTRACTION. THE LOWER SECTION SHOWS THE MAXIMAL VELOCITY AND MAXIMAL FORCE OBTAINED FROM THE LINEAR SYSTEM.

COMPUTER PROGRAM USED TO CALCULATE MEANS AND STANDARD DEVIATIONS (SD)

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      ∇DSTAT[[]]∇
    ∇ DSTAT X;R;MAX;MIN;N;MEAN;VAR;SD;MD;MED;V;M
[1]   SD←(VAR←(+/(X-MEAN←(+/X)÷N)*2)÷(N←⍴X)-1)*0.5
[2]   'MEAN                    ', 6 1 ▼MEAN
[3]   'STANDARD.DEVIATION      ', 5 1 ▼SD
    ∇
```

DENERVATED: GROUP 1

FORCE (gm)	VELOCITY (cm/sec) RAT 1	RAT 2	RAT 3	MEAN	SD
0	0.0	0.0	0.0	0.0	0.0
50	1.8	1.5	2.0	1.6	0.2
100	1.4	1.7	2.0	1.7	0.3
150	0.3	1.3	1.0	0.9	0.5
200	0.0	0.3	0.4	0.4	0.1
250	0.0	0.0	0.0	0.0	0.0
LINEAR VELOCITY:	1.6	2.5	2.6	2.2	0.6
LINEAR FORCE:	192	282	234	236.0	45.0

DENERVATED: GROUP 2

FORCE (gm)	VELOCITY (cm/sec) RAT 4	RAT 5	MEAN	SD
0	0.0	0.0	0.0	0.0
10	0.2	0.3	0.3	0.1
20	0.5	0.4	0.4	0.1
30	0.5	0.3	0.4	0.1
40	0.4	0.3	0.4	0.1
50	0.3	0.3	0.3	0.0
60	0.2	0.1	0.1	0.1
70	0.0	0.0	0.0	0.0
LINEAR VELOCITY:				
	0.8	0.8	0.8	0.0
LINEAR FORCE:				
	75	71	73.0	2.8

DENERVATED: GROUP 3

FORCE (gm)	VELOCITY (cm/sec) RAT 6	MEAN	SD
0	0.0	0.0	0.0
150	4.5	4.5	0.0
300	4.1	4.1	0.0
450	3.9	3.9	0.0
600	2.2	2.2	0.0
750	2.0	2.0	0.0
900	1.2	1.2	0.0
1050	0.4	0.4	0.0
1200	0.1	1.1	0.0
1250	0.0	0.0	0.0
LINEAR VELOCITY:			
	6.9	6.9	0.0
LINEAR FORCE:			
	1247	1247	0.0

SEDENTARY GROUP

VELOCITY (cm/sec)

FORCE (gm)	RAT 1	RAT 2	RAT 3	RAT 4	RAT 5	MEAN	SD
0	0	0	0	0	0	0	
200	4.0	6.5	10.3	8.3	7.8	7.4	2.3
300	9.2	9.3	12.9	10.6	9.8	10.3	1.5
400	11.2	9.5	13.2	8.4	11.0	10.7	1.8
600	9.0	8.1	10.5	6.0	11.4	9.0	2.1
800	5.7	6.8	6.3	4.6	10.4	6.8	2.2
1000	5.1	6.4	4.3	3.4	10.0	5.8	2.6
1200	4.8	5.6	3.9	2.7	9.4	5.3	2.5
1400	4.6	3.9	3.3	2.3	6.9	4.2	1.7
1600	3.6	3.1	2.9	2.3	5.3	3.4	1.1
1800	2.0	1.8	2.4	1.9	4.5	2.5	1.1
2000	1.3	0.9	1.7	1.7	3.5	1.8	1.0
2200	0.7	0.3	0.9	1.4	2.7	1.2	0.9
2400	0.3	0.1	0.3	0.9	1.7	0.7	0.6
2600	0.1	0	0	0.4	0.8	0.3	0.3
2668	0	0	0	0	0	0	0
LINEAR VELOCITY:							
	9.5	10.5	11.1	12.0	11.6	10.8	1.0
LINEAR FORCE:							
	2615	2480	2600	2934	2711	2668.0	169.8

TRAINED: GROUP 1

	VELOCITY (cm/sec)			
FORCE (gm)	RAT 1	RAT 2	MEAN	SD
0	0	0	0	0
200	5.5	9.9	7.7	3.1
400	6.6	12.1	9.4	3.8
600	5.3	7.6	6.5	1.6
800	4.5	3.6	4.0	0.7
1000	3.1	2.3	2.7	0.6
1200	1.9	2.2	2.1	0.3
1400	0.6	1.4	1.0	0.3
1600	0.2	0.8	0.5	0.4
1758	0	0	0	0
LINEAR VELOCITY:	6.8	6.7	6.8	0.1
LINEAR FORCE:	1800	1715	1757.5	60.1

TRAINED: GROUP 2

	VELOCITY (cm.sec)					
FORCE (gm)	RAT 3	RAT 4	RAT 5	RAT 6	MEAN	SD
0	0	0	0	0	0	
200	10.0	8.7	13.5	15.6	11.9	3.0
300	16.0	14.3	16.1	16.9	15.8	1.1
400	15.1	20.1	10.7	12.9	14.7	4.1
600	10.7	8.4	6.0	8.1	8.3	1.9
800	8.3	5.0	4.9	5.8	6.0	1.6
1000	6.2	4.8	4.8	4.2	5.0	0.8
1200	5.0	4.5	4.2	3.5	4.3	0.6
1400	4.2	4.3	3.5	2.9	3.7	0.7
1600	3.2	3.8	3.2	2.5	3.2	0.5
1800	2.3	2.4	2.7	2.4	2.5	0.2
2000	1.0	2.2	2.1	2.1	1.9	0.6
2200	0.2	1.6	1.1	1.3	1.1	0.3
2400	0	1.0	0	0.8	0.5	0.3
2560	0	0	0	0	0	0
LINEAR VELOCITY:						
	12.9	12.3	12.3	14.0	12.9	0.8
LINEAR FORCE:						
	2240	2867	2400	2734	2560.3	290.1

APPENDIX 5: MEANS AND STANDARD DEVIATIONS OF COMPLIANCE CORRESPONDING TO THE LEVELS OF FORCE PRODUCED DURING ISOMETRIC CONTRACTION. THE LOWER SECTION SHOWS THE VALUES OF COMPLIANCE OBTAINED FROM THE LINEAR SYSTEM.

DENERVATED: GROUP 1

	COMPLIANCE (cm/Kg)				
FORCE (gm)	RAT 1	RAT 2	RAT 3	MEAN	SD
0	0	0	0	0	0
50	0.47	0.56	0.47	0.52	0.09
100	0.45	0.51	0.55	0.51	0.04
150	0.20	0.36	0.36	0.31	0.09
200	0	0.15	0.32	0.16	0.16
236	0	0	0	0	0

LINEAR COMPLIANCE:

0.35	0.47	0.54	0.45	0.10

DENERVATED: GROUP 2

COMPLIANCE (cm/Kg)

FORCE (gm)	RAT 4	RAT 5	MEAN	SD
0	0	0	0	0
12.5	0.35	0.40	0.38	0.04
25.0	0.43	0.80	0.62	0.26
37.5	0.39	0.75	0.57	0.26
50.0	0.35	0.75	0.55	0.28
62.5	0.13	0.66	0.40	0.38
73.0	0	0	0	0
LINEAR COMPLIANCE:				
	0.53	0.49	0.51	0.03

DENERVATED: GROUP 3

	COMPLIANCE (cm/Kg)		
FORCE (gm)	RAT 6	MEAN	SD
0	0	0	0
250	0.30	0.30	0
500	0.22	0.22	0
750	0.22	0.22	0
1000	0.16	0.16	0
1247	0	0	0
LINEAR COMPLIANCE:			
	0.26	0.26	0

SEDENTARY GROUP

COMPLIANCE (cm/Kg)

FORCE (gm)	RAT 1	RAT 2	RAT 3	RAT 4	RAT 5	MEAN	SD
0	0	0	0	0	0	0	0
200	0.14	0.14	0.40	0.25	0.34	0.25	0.12
300	0.28	0.32	0.49	0.28	0.36	0.35	0.09
400	0.31	0.32	0.48	0.24	0.38	0.35	0.09
600	0.28	0.27	0.39	0.19	0.37	0.30	0.08
800	0.21	0.28	0.23	0.15	0.31	0.23	0.06
1000	0.19	0.24	0.17	0.11	0.29	0.20	0.07
1200	0.21	0.22	0.16	0.09	0.28	0.19	0.08
1400	0.24	0.19	0.15	0.08	0.23	0.18	0.07
1600	0.24	0.21	0.15	0.08	0.20	0.18	0.06
1800	0.16	0.18	0.14	0.09	0.19	0.15	0.04
2000	0.12	0.13	0.14	0.09	0.18	0.13	0.03
2200	0.09	0.08	0.09	0.10	0.17	0.11	0.04
2400	0	0	0.05	0.10	0.15	0.06	0.05
2600	0	0	0	0.09	0.11	0.04	0.04

LINEAR COMPLIANCE:

	0.23	0.26	0.26	0.23	0.24	0.24	0.01

TRAINED: GROUP 1

COMPLIANCE (cm/Kg)

FORCE (gm)	RAT 1	RAT 2	MEAN	SD
0	0	0	0	0
200	0.89	0.36	0.63	0.37
400	1.01	0.36	0.69	0.46
600	0.60	0.34	0.47	0.18
800	0.29	0.33	0.31	0.03
1000	0.22	0.30	0.26	0.06
1200	0.24	0.23	0.24	0.01
1400	0.14	0.20	0.17	0.04
1600	0.09	0.17	0.13	0.06
1757	0	0	0	0

LINEAR COMPLIANCE:

0.34	0.29	0.32	0.04

TRAINED: GROUP 2

COMPLIANCE (cm/Kg)

FORCE (gm)	RAT 3	RAT 4	RAT 5	RAT 6	MEAN	SD
0	0	0	0	0	0	0
200	0.48	0.38	0.61	0.54	0.50	0.10
300	0.74	0.60	0.60	0.53	0.62	0.09
400	0.65	0.74	0.40	0.43	0.56	0.17
600	0.49	0.27	0.21	0.26	0.30	0.12
800	0.39	0.18	0.17	0.20	0.24	0.10
1000	0.29	0.17	0.18	0.14	0.20	0.07
1200	0.23	0.16	0.20	0.12	0.18	0.05
1400	0.20	0.16	0.19	0.12	0.17	0.04
1600	0.21	0.18	0.21	0.11	0.18	0.06
1800	0.26	0.12	0.21	0.13	0.18	0.07
2000	0.19	0.14	0.20	0.14	0.17	0.03
2200	0	0.12	0.14	0.12	0.10	0.03
2400	0	0.11	0	0.09	0.05	0.04
2560	0	0	0	0	0	0
LINEAR COMPLIANCE:						
	0.36	0.31	0.30	0.33	0.32	0.03

APPENDIX 6: MEAN VALUES FOR THE PASSIVE, ACTIVE AND TOTAL FORCES CORRESPONDING TO DIFFERENT MUSCLE LENGTHS (ZERO REFERS TO RESTING LENGTH L_o).

DENERVATED: GROUP 1

LENGTH (mm)	PASSIVE FORCE (gm)		ACTIVE FORCE (gm)		TOTAL FORCE (gm)	
	RAT 1	MEAN	RAT 1	MEAN	RAT 1	MEAN
-3.5	0	0	500	500	500	500
-2.8	0	0	530	530	530	530
-2.1	0	0	530	530	530	530
-1.4	0	0	530	530	530	530
-0.7	0	0	520	520	520	520
0	20	20	480	480	500	500
0.7	30	30	450	450	480	480
1.4	50	50	450	450	500	500
2.1	200	200	370	370	570	570
2.8	430	430	270	270	700	700
3.5	630	630	200	200	830	830
4.2	630	630	170	170	800	800
4.9	670	670	130	130	800	800
5.6	1170	1170	60	60	1230	1230
6.3	1630	1630	40	40	1670	1670
7.0	1970	1970	20	20	1990	1990

DENERVATED: GROUP 2

LENGTH (mm)	PASSIVE FORCE (gm)			ACTIVE FORCE (gm)			TOTAL FORCE (gm)		
	RAT 1	RAT 2	MEAN	RAT 1	RAT 2	MEAN	RAT 1	RAT 2	MEAN
-3.5	0	0	0	90	126	108	90	126	108
-2.8	0	0	0	100	160	130	100	160	130
-2.1	0	0	0	116	150	133	116	150	133
-1.4	0	0	0	100	160	130	100	160	130
-0.7	0	0	0	110	160	135	110	160	135
0	6	10	8	80	130	105	86	140	113
0.7	40	46	43	76	110	93	116	156	136
1.4	110	120	115	40	76	58	150	196	173
2.1	300	280	290	36	50	43	336	330	333
2.8	620	550	585	20	30	25	640	580	610
3.5	1060	980	1020	0	20	10	1060	1000	1030
4.2	1200	1080	1140	0	0	0	1200	1080	1140
4.9	1240	1140	1190	0	0	0	1240	1140	1190
5.6	1410	1580	1665	0	0	0	1410	1580	1665

SEDENTARY: GROUP 1

LENGTH (mm)	PASSIVE FORCE (gm)			ACTIVE FORCE (gm)			TOTAL FORCE (gm)		
	RAT 1	RAT 2	MEAN	RAT 1	RAT 2	MEAN	RAT 1	RAT 2	MEAN
-3.5	0	0	0	1350	1450	1400	1350	1450	1400
-2.8	0	0	0	1630	1450	1540	1630	1450	1540
-2.1	0	0	0	1800	1480	1740	1800	1480	1640
-1.4	0	0	0	1950	1750	1850	1950	1750	1850
-0.7	0	0	0	1950	1680	1815	1950	1680	1815
00	10	30	20	2040	1620	1830	2050	1650	1850
0.7	30	30	30	2000	1600	1800	2030	1630	1830
1.4	30	40	35	1870	1540	1705	1900	1580	1760
2.1	50	60	55	1800	1420	1610	1850	1480	1665
2.8	80	130	105	1700	1270	1485	1780	1400	1590
3.5	150	180	165	1500	1120	1310	1650	1300	1475
4.2	260	300	280	1270	1100	1185	1530	1400	1465
4.9	490	480	485	910	800	855	1400	1280	1340
5.6	700	630	665	730	770	750	1430	1400	1415
6.3	1080	880	980	400	600	500	1480	1580	1530
7.0	1480	1350	1415	350	330	340	1830	1680	1755
7.7	1980	1700	1840	100	130	115	2080	1830	1955
8.4	2100	2180	2140	50	70	60	2150	2250	2200

SEDENTARY: GROUP 2

LENGTH (mm)	PASSIVE FORCE (gm)			ACTIVE FORCE (gm)			TOTAL FORCE (gm)		
	RAT 3	RAT 4	MEAN	RAT 3	RAT 4	MEAN	RAT 3	RAT 4	MEAN
-3.5	0	0	0	1850	2100	1975	1850	2100	1975
-2.8	0	0	0	1880	2180	2030	1880	2180	2030
-2.1	0	0	0	1890	2300	2140	1890	2300	2140
-1.4	0	0	0	2130	2380	2255	2130	2380	2255
-0.7	0	0	0	2030	2250	2140	2050	2250	2140
0	10	30	20	2090	2300	2240	2100	2330	2215
0.7	130	100	115	1990	2080	2035	2120	2180	2150
1.4	250	230	240	1500	1820	1660	1750	2050	1900
2.1	380	350	365	1250	1600	1425	1650	1950	1800
2.8	500	480	490	1060	1370	1165	1560	1850	1705
3.5	750	800	775	880	1250	1065	1630	2050	1840
4.2	930	980	955	810	1000	905	1740	1980	1860
4.9	1630	1700	1665	500	550	525	2130	2250	2190
5.6	2280	2330	2305	250	450	350	2530	2780	2655
6.3		2600	2600		180	180		2780	2780

TRAINED GROUP

LENGTH (mm)	PASSIVE FORCE (gm)			ACTIVE FORCE (gm)			TOTAL FORCE (gm)		
	RAT 1	RAT 2	MEAN	RAT 1	RAT 2	MEAN	RAT 1	RAT 2	MEAN
-3.5	0	0	0	2100	2000	2050	2100	2000	2050
-2.8	0	0	0	2170	2300	2235	2170	2300	2235
-2.1	0	0	0	2200	2400	2300	2200	2400	2300
-1.4	0	0	0	2330	2370	2350	2330	2370	2350
-0.7	0	0	0	2270	2330	2300	2270	2330	2300
0	30	30	30	2070	2170	2120	2100	2200	2150
0.7	40	50	45	1990	1950	1970	2030	2000	2015
1.4	70	100	85	1900	1670	1785	1970	1770	1870
2.1	130	230	180	1700	1370	1545	1830	1600	1715
2.8	300	400	350	1230	1070	1150	1530	1470	1500
3.5	370	730	550	1000	770	935	1370	1500	1435
4.2	600	1150	875	700	520	610	1300	1670	1485
4.9	1000	1770	1335	470	280	375	1470	2050	1760
5.6	1870	2230	2050	160	100	130	2030	2330	2180
6.3	2170	2570	2370	60	60	60	2230	2630	2430
7.0	2530		2530	40		40	2570		2570

APPENDIX 7: INTEGRATED VALUES OF EXTENSION AND STANDARD DEVIATIONS CORRESPONDING TO THE LEVELS OF FORCE PRODUCED DURING ISOMETRIC CONTRACTION (SEE TEXT).

DENERVATED: GROUP 1

FORCE (gm)	EXTENSION (cm)	SD
0	0	0
50	.013	±.002
100	.039	±.005
150	.059	±.009
200	.071	±.015

DENERVATED: GROUP 2

FORCE (gm)	EXTENSION (cm)	SD
0	0	0
12.5	.0024	±.0002
25.0	.0087	±.0072
27.5	.016	±.011
50.0	.023	±.015
62.5	.029	± 0.19

SEDENTARY GROUP

FORCE (gm)	EXTENSION (cm)	SD
0	0	0
200	.025	±.007
400	.090	±.028
600	.155	±.045
800	.208	±.059
1000	.251	±.072
1200	.290	±.087
1400	.327	±.102
1600	.353	±.125
1800	.396	±.125
2000	.424	±.132
2200	.448	±.139
2400	.465	±.148
2600	.475	±.157

TRAINED: GROUP 2

FORCE (gm)	EXTENSION (cm)	SD
0	0	0
200	.050	±.010
400	.156	±.037
600	.242	±.066
800	.296	±.088
1000	.340	±.105
1200	.378	±.117
1400	.413	±.126
1600	.448	±.136
1800	.484	±.149
2000	.519	±.159
2200	.546	±.165
2400	.561	±.172

APPENDIX 8: STATISTICAL ANALYSIS OF ANATOMICAL MEASUREMENTS

LEGEND FOR ANALYSIS OF VARIANCE

TABLE 1

NUMBER	GROUP 1		GROUP 2		GROUP 3	
	B_1	B_1^2	B_2	B_2^2	B_3	B_3^2
1						
2						
3						
4						
5						
	-sum of B_1	of B_1^2	of B_2	of B_2^2	of B_3	of B_3^2

n_1 = number in group 1

$\bar{x} = \frac{B_1}{n_1}$ n_2 = $\bar{x} = \frac{B_2}{n_2}$ n_3 = $\bar{x} = \frac{B_3}{n_3}$

= mean value for group 1

$$\Sigma x_{TOT} = \Sigma B_1 + \Sigma B_2 + \Sigma B_3$$

$$\Sigma x^2_{TOT} = \Sigma B_1^2 + \Sigma B_2^2 + \Sigma B_3^3$$

$$N = n_1 + n_2 + n_3$$

TABLE 2

SOURCE OF VARIATION	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	$\Sigma x^2_B = \frac{\Sigma xi}{ni}^2 - \frac{\Sigma x_{TOT}}{N}^2$	$df_B = k-1$ where k=# of groups	$S^2_B = \Sigma x^2_B / df_B$	$F = \frac{S^2_B}{S^2_W}$
WITHIN GROUPS (W)	$\Sigma x^2_W = \Sigma x^2_i - \frac{\Sigma xi}{ni}^2$ or $= \Sigma x^2_{TOT} - \Sigma x^2_B$	$df_W = N-k$	$S^2_W = x^2_W / df_W$	$df = df_B / df_W$ for F ratio tables
TOTAL	$\Sigma x^2_{TOT} = \Sigma x^2_{TOT} - \frac{\Sigma x_{TOT}}{N}^2$	$df_{TOT} = df_B + df_W$ or N - 1		

INTERPRETATION OF F -- A difference between two means is significant, at a given α-level, if it equals or exceeds HSD, which is

$$HSD = q_\alpha \frac{S^2_W}{n}$$

where HSD = honestly significant difference.

S^2_W = the within group variance estimate.

n = number of subjects in each group.

q_α = table value for a given α-level corresponding to df_W and k.

BODY WEIGHT (BW)

	DENERVATED		SEDENTARY		TRAINED	
	BW_1	BW_1^2	BW_2	BW_2^2	BW_3	BW_3^2
1	593.8	352588.4	656.3	430729.7	774.8	600315.0
2	668.7	447159.7	765.9	586602.8	579.9	336284.0
3	709.0	502681.0	689.3	487622.9	678.1	459819.6
4	602.4	362885.8	705.0	497025.0	662.6	439038.8
5	617.0	380689.0	612.4	375033.8	700.0	490000.0
6	634.1	402082.8	521.0	271441.0	683.7	467445.7
7	585.3	342576.1	547.1	299318.4	579.5	335820.3
8	544.3	296252.5	583.6	340588.9	563.9	317983.2
9	655.6	429811.4	597.7	357245.3		
10						
TOTAL	5610.2	3516736.7	5687.3	3645607.8	5222.5	3446706.6
	$n_1=9$	$\overline{BW}_1=623.4$	$n_2=9$	$\overline{BW}_2=631.9$	$n_3=8$	$\overline{BW}_3=652.8$

$$\Sigma BW_{TOT} = 16520$$

$$\Sigma BW^2_{TOT} = 10609051.1$$

$$N = 26$$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	3840.7	2	1920.35	0.406
WITHIN GROUPS (W)	108657.4	23	4724.2	
TOTAL	112498.1	25		

$F = 0.406 < 3.42$ for the $df_{B/W}$ of 2/23, no significant difference at the F level of 0.05.

MUSCLE WEIGHT (MW)

	DENERVATED		SEDENTARY		TRAINED	
	MW_1	MW_1^2	MW_2	MW_2^2	MW_3	MW_3^2
1	3.0760	9.4618	5.0391	25.3925	5.6387	31.7949
2	3.1662	10.0248	4.9427	24.2527	5.4672	29.8903
3	2.9710	8.8268	4.6900	21.9961	5.6544	31.9722
4	2.6546	7.0469	5.1427	26.4474	5.8803	34.5779
5			4.8281	23.3105	5.6790	32.2510
6			4.9963	24.9630	5.5158	30.4240
7			5.0602	25.6056	5.2530	27.5940
8			5.1338	26.3559	4.8271	23.3009
9			4.8407	23.4324		
TOTAL	11.8678	35.3603	44.6556	221.7561	43.9155	241.8052
	$n_1=4$	$\overline{MW}_1=2.9669$	$n_2=9$	$\overline{MW}_2=4.9617$	$n_3=8$	$\overline{MW}_3=5.4894$

$$\Sigma MW_{TOT} = 100.4389$$

$$\Sigma MW^2_{TOT} = 498.9216$$

$$N = 21$$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	17.4722	2	8.7361	144.0724
WITHIN GROUPS (W)	1.0698	18	0.0594	
TOTAL	18.5420	20		

$F = 141.0724 \geq 6.01$ for the $df_{B/W}$ of 2/18, there is a significant difference at the F level of 0.01.

INTERPRETATION OF F

	$\overline{MW}_1$	$\overline{MW}_2$	$\overline{MW}_3$
$\overline{MW}_1$ (2.9669)	--	1.9948	2.5225
$\overline{MW}_2$ (4.9617)	--	--	0.5277
$\overline{MW}_3$ (5.4894)	--	--	--

$df_w = 18$

$K = 3$

$\alpha 0.01 = 4.70$

$HSD_{0.01} = 0.5727$ for denervated group

$HSD_{0.01} = 0.4050$ for trained group

$1.9948 \geq 0.5727$

$0.5277 \geq 0.4050$

Therefore both treatments had a significant effect on MW at the α-level of 0.01.

MUSCLE WEIGHT (MW)

	DENERVATED (2 MONTHS)		SEDENTARY		TRAINED	
	MW_1	MW_1^2	MW_2	MW_2^2	MW_3	MW_3^2
1	3.0760	9.4618	5.0391	25.3925	2.2362	5.0006
2	3.1662	10.0428	4.9247	24.2527	2.4167	5.8404
3	2.9710	8.8268	4.6900	21.9961	1.9340	3.7404
4	2.6546	7.0469	5.1427	26.4474	2.4074	5.7956
5			4.8281	23.3105		
6			4.9963	24.9630		
7			5.0602	25.6056		
8			5.1338	26.3559		
9			4.8407	23.4324		
TOTAL	11.8678	35.3603	44.6556	221.7561	8.9943	20.3770
	$n_1=4$	$\overline{MW}_1=2.9669$	$n_2=9$	$\overline{MW}_2=4.9617$	$n_3=4$	$\overline{MW}_3=2.2486$

$$\Sigma MW_{TOT} = 65.5177$$

$$\Sigma MW^2_{TOT} = 277.4934$$

$$N = 17$$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	24.5008	2	12.2504	351.0143
WITHIN GROUPS (W)	0.4886	14	0.0349	
TOTAL	24.9894	16		

$F = 351.0143 \geq 6.51$ for the $df_{B/W}$ of 2/14, there is a significant difference at the F -level of 0.01.

INTERPRETATION OF F

	$\overline{MW}_1$	$\overline{MW}_2$	$\overline{MW}_3$
$\overline{MW}_1$	--	1.9948	0.7183
$\overline{MW}_2$	--	--	2.7131
$\overline{MW}_3$	--	--	--

$df_w = 14$

$K = 3$

$\alpha 0.01 = 4.89$

$HSD_{0.01} = 0.4568$

$1.9948 \geq 0.4568$

$0.7183 \geq 0.4568$

$2.7131 \geq 0.4568$

Both denervated groups presented MWs which were significantly different than the sedentary and each other at the α-level of 0.01.

MUSCLE LENGTH (ML)

	DENERVATED (1 MONTH)		SEDENTARY		TRAINED	
	ML_1	ML_1^2	ML_2	ML_2^2	ML_3	ML_3^2
1	5.3	28.09	5.2	27.04	5.2	27.04
2	5.4	29.16	5.3	28.09	5.2	27.04
3	5.9	34.81	5.2	27.04	5.3	28.09
4	5.8	33.64	5.3	28.09	5.2	27.04
5			5.3	28.09	5.3	28.09
6			5.2	27.04	5.1	26.01
7			5.2	27.04	5.2	27.04
8			5.2	27.04	5.1	26.01
9			5.2	27.04		
TOTAL	22.40	125.70	47.10	246.61	41.60	216.36
	$n_1=4$	$\overline{ML}_1=5.6$	$n_2=9$	$\overline{ML}_2=5.23$	$n_3=8$	$\overline{ML}_3=5.2$

$$\Sigma ML_{TOT} = 111.10$$

$$\Sigma ML^2_{TOT} = 588.57$$

$$N = 21$$

SOURCES OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	0.48	2	0.24	13.33
WITHIN GROUPS (W)	0.32	18	0.018	
TOTAL	0.80	20		

$F = 13.33 \geq 6.01$ for the $df_{B/W}$ of 2/18, there is a significant difference at the F level of 0.01.

INTERPRETATION OF F

	$\overline{ML}_1$	$\overline{ML}_2$	$\overline{ML}_3$
$\overline{ML}_1$	--	0.37	0.40
$\overline{ML}_2$	--	--	0.03
$\overline{ML}_3$	--	--	--

$df_w = 18$

$K = 3$

$\alpha 0.01 = 4.70$

$$HSD_{0.01} = 0.32$$

$0.37 \geq 0.32$ -- The denervated group demonstrated a $\overline{ML}$ which was significantly different that that of the sedentary group at an α-level of 0.01.

-- There was no significant difference between the $\overline{ML}$s of the trained and sedentary groups.

MUSCLE LENGTH (ML)

	DENERVATED (1 MONTH)		SEDENTARY		DENERVATED (2 MONTHS)	
	ML_1	ML_1^2	ML_2	ML_2^2	ML_3	ML_3^2
1	5.3	28.09	5.2	27.04	5.8	33.64
2	5.4	29.16	5.3	28.09	5.8	33.64
3	5.9	34.81	5.2	27.04	5.7	32.49
4	5.8	33.64	5.3	28.09	5.8	33.64
5			5.3	28.09		
6			5.2	27.04		
7			5.2	27.04		
8			5.2	27.04		
9			5.2	27.04		
TOTAL	22.40	125.70	47.10	246.51	23.10	133.41
	$n_1=4$	$\overline{ML}_1=5.6$	$n_2=9$	$\overline{ML}_2=5.23$	$n_3=4$	$\overline{ML}_3=5.8$

$$\Sigma ML_{TOT} = 92.60$$

$$\Sigma ML^2_{TOT} = 505.62$$

$$N = 17$$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	0.94	2	0.47	23.5
WITHIN GROUPS (W)	0.29	14	0.02	
TOTAL	1.23	16		

$F = 23.5 \geq 6.51$ for the $df_{B/W}$ of 2/14, there is a significant difference at the F -level of 0.01.

INTERPRETATION OF F

	$\overline{ML}_1$	$\overline{ML}_2$	$\overline{ML}_3$
$\overline{ML}_1$	--	0.37	0.20
$\overline{ML}_2$	--	--	0.57
$\overline{ML}_3$	--	--	--

$df_w = 14$

$K = 3$

$\alpha 0.01 = 4.89$

$HSD_{0.01} = 0.34$ for both denervated groups

$0.37 \geq 0.34$

$0.57 \geq 0.34$

Both denervated groups demonstrated $\overline{ML}$s which were significantly different than those of the sedentary group at an α-level of 0.01. There was no significant difference between the denervated groups.

APPENDIX 9: STATISTICAL ANALYSIS OF THE CALCULATED LINEAR PARAMETERS.

SLOPE OF THE LINEAR FORCE-VELOCITY RELATIONSHIPS (B)

	DENERVATED (1 MONTH)		SEDENTARY		TRAINED	
	B_1	B_1^2	B_2	B_2^2	B_3	B_3^2
1	123.08	15148.69	274.11	75136.29	173.91	30244.69
2	114.17	13034.79	237.09	56211.67	233.09	54330.95
3	90.00	8100.00	234.02	54765.36	195.92	38384.65
4			243.89	59482.33	195.98	38408.16
5			234.11	54807.49		
TOTALS	327.25	36282.48	1223.22	300403.14	789.90	161368.45
	$n_1=3$	$\overline{B}_1=109.08$	$n_2=5$	$\overline{B}_2=244.64$	$n_3=4$	$\overline{B}_3=199.73$

$\Sigma B_{TOT} = 2349.37$

$\Sigma B_{TOT}^2 = 498054.07$

$N = 12$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	34549.64	2	17274.82	43.88
WITHIN GROUPS (W)	3542.82	9	393.65	
TOTAL	38092.47	11		

$F = 43.88 \geq 8.02$ for the $df_{B/W}$ of 2/9, there is a significant difference at an F -level of 0.01.

INTERPRETATIONS OF F

	$\overline{B}_1$	$\overline{B}_2$	$\overline{B}_3$
$\overline{B}_1$(109.08)	--	135.56	90.65
$\overline{B}_2$(244.64)	--	--	44.91
$\overline{B}_3$(199.73)	--	--	--

$df_W = 9$

$K = 3$

$\alpha 0.01 = 5.43$

$\alpha 0.05 = 3.95$

$HSD_{0.01}$ = 62.17 for the denervated (1 month group)

$HSD_{0.05}$ = 39.18 for the trained group.

$135.56 \geq 62.17$ -- Significant difference between the $\overline{B}$ value of the sedentary and denervated groups at an α-level of 0.01.

$44.91 \geq 39.18$ -- Difference between $\overline{B}$ values of the sedentary and trained groups at an α-level of 0.05.

VELOCITY AXIS INTERCEPT OF THE LINEAR F/V RELATIONSHIPS

	DENERVATED (1 MONTH)		SEDENTARY		TRAINED	
	V_1	V_1^2	V_2	V_2^2	V_3	V_3^3
1	1.56	2.43	9.54	91.01	12.88	165.89
2	2.47	6.10	10.46	109.41	12.30	151.29
3	2.60	6.76	11.11	123.43	12.25	150.06
4			12.03	144.72	13.95	194.60
5			11.58	134.10		
TOTAL	6.63	15.29	54.72	602.67	51.38	661.84
	$n_1=3$	$\bar{V}_1=2.21$	$n_2=5$	$\bar{V}_2=10.94$	$n_3=4$	$\bar{V}=12.85$

$$\Sigma V_{TOT} = 112.73$$

$$\Sigma V_{TOT}^2 = 1279.80$$

$$N = 12$$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	214.48	2	107.24	153.20
WITHIN GROUPS (W)	6.32	9	0.70	
TOTAL	220.80	11		

$F = 153.20 \geq 8.02$ for the $df_{B/W}$ of 2/9, there is a significant difference at an F -level of 0.01.

INTERPRETATION OF F

	$\bar{V}_1$	$\bar{V}_2$	$\bar{V}_3$
$\bar{V}_1$(2.21)	--	8.73	10.64
$\bar{V}_2$(10.94)	--	--	1.91
$\bar{V}_3$	--	--	--

$df_w = 9$
$K = 3$
$\alpha 0.01 = 5.43$
$\alpha 0.05 = 3.95$

$HSD_{0.01}$ = 2.62 for the denervated group

$HSD_{0.05}$ = 1.65 for the trained group

$8.73 \geq 2.62$ -- Difference between the $\overline{V}$ values of the denervated and sedentary groups at an α-level of 0.01.

$1.91 \geq 1.65$ -- Significant difference between the $\overline{V}$ values of the sedentary and trained groups at an α-level of 0.05.

FORCE AXIS INTERCEPT OF THE LINEAR F/V RELATIONSHIPS

	DENERVATED (1 MONTH)		SEDENTARY		TRAINED	
	F_1	F_1^2	F_2	F_2^2	F_3	F_3^2
1	192	36864	2615	6838225	2240	5017600
2	282	79524	2600	6760000	2867	8219689
3	232	53824	2480	6150400	2400	5760000
4			2934	8608356	2734	7474756
5			2711	7349521		
TOTAL	706	170212	13340	35706502	10241	26472045
	$n_1=3$	$\bar{F}_1=235$	$n_2=5$	$\bar{F}_2=2668$	$n_3=4$	$\bar{F}_3=2560$

$\Sigma F_{TOT} = 24287$

$\Sigma F^2_{TOT} = 62348759$

$N = 12$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREE OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	12822130	2	6411065	155.12
WITHIN GROUPS (W)	371969	9	41330	
TOTAL	13194099	11		

$F = 155.12 \geq 8.02$ for a $df_{B/W}$ of 2/9, there is a significant difference at an F -level of 0.01.

INTERPRETATION OF F

	$\bar{F}_1$	$\bar{F}_2$	$\bar{F}_3$
$\bar{F}_1$	--	2433	2325
$\bar{F}_2$	--	--	108
$\bar{F}_3$	--	--	--

$df_W = 9$

$K = 3$

$\alpha 0.01 = 5.43$

$\alpha 0.05 = 3.95$

$HSD_{0.01} = 637.32$

$HSD_{0.05} = 401.52$

$2433 \geq 637.32$ -- There was a significant difference between the $\overline{F}$ values of the denervated and sedentary groups at an α -level of 0.01.

$108 \not\geq 401.52$ -- There was no significant difference between the $\overline{F}$ values of the sedentary and trained groups.

COMPLIANCE (C)

	DENERVATED (1 MONTH)		SEDENTARY		TRAINED	
	C_1	C_1^2	C_2	C_2^2	C_3	C_3^2
1	.000346	.0000001197	.000232	.0000000538	.000362	.0000001310
2	.000472	.0000002228	.000258	.0000000673	.000308	.0000000949
3	.000544	.0000002959	.000257	.0000000661	.000296	.0000000877
4			.000230	.0000000529	.000328	.0000001076
5			.000241	.0000000581		
TOTAL	.001362	.0000006384	.001218	.0000002982	.001294	.0000004212
	$n_1=3$	$\bar{C}_1=.000454$	$n_2=5$	$\bar{C}_2=.000244$	$n_3=4$	$\bar{C}_3=.000324$

$$\Sigma C_{TOT} = 0.003874$$

$$\Sigma C_{TOT}^2 = 0.000001365$$

$$N = 12$$

SOURCE OF VARIANCE	SUM OF SQUARES	DEGREES OF FREEDOM	VARIABLE ESTIMATE	F
BETWEEN GROUPS (B)	.0000000836	2	.0000000418	16.08
WITHIN GROUPS (W)	.0000000234	9	.0000000026	
TOTAL	.0000001170	11		

$F = 16.08 \geq 8.02$ for $df_{B/W}$ of 2/9, there is a significant difference at an F -level of 0.01.

INTERPRETATION OF F

	$\bar{C}_1$	$\bar{C}_2$	$\bar{C}_3$
$\bar{C}_1$(.000454)	--	.000210	.000130
$\bar{C}_2$(.000244)	--	--	.000080
$\bar{C}_3$(.000324)	--	--	--

$df_w = 9$

$K = 3$

$\alpha 0.01 = 5.43$

$\alpha 0.05 = 3.95$

$HSD_{0.01} = .000159$

$HSD_{0.05} = .000101$

$.000210 \geq .000159$ -- A significant difference between the $\bar{C}$ values of the denervated and sedentary group existed at an αlevel of 0.01.

$0.000101 \geq .000080$ -- No significant difference between the sedentary and trained group. This result was disputed by the graphic representation of the standard deviation curves of the groups. Additional analysis is necessary.

	SEDENTARY			TRAINED		
	C_1	DEVIATION FROM MEANS	DEVIATIONS^2	C_2	DEVIATION	DEVIATION^2
1	.000232	.000012	.000000000144	.000362	.000038	.000000001444
2	.000258	.000014	.000000000196	.000308	.000016	.000000000256
3	.000257	.000013	.000000000169	.000296	.000028	.000000000784
4	.000230	.000006	.000000000036	.000328	.000004	.000000000016
5	.000241	.000003	.000000000009			

$\bar{C}_1 = .000244$ $\bar{C}_2 = .000324$

$\Sigma x^2 = .000000000554$ $\Sigma y^2 = .0000000025$

$n_{C_1} = 5$ $n_{C_2} = 4$

$$= \frac{\bar{C}_1 - \bar{C}_2}{\sqrt{\frac{\Sigma x^2 + \Sigma y^2}{n_{C_1} + n_{C_2} - 2} \cdot \frac{n_{C_1} + n_{C_2}}{n_{C_1} \times n_{C_2}}}}$$

$$= \frac{.000244 - .000324}{\sqrt{\frac{5.54 \times 10^{-10} + 25 \times 10^{-10}}{7} \cdot \frac{9}{20}}}$$

$= 5.71$

$5.71 \geq 3.250$

$\therefore$ There was a significant difference between the $\bar{G}$ values of the sedentary and trained groups at an α-level of 0.01.