GENDER DIFFERENCES IN STRENGTH AND MUSCLE CHARACTERISTICS

GENDER DIFFERENCES IN STRENGTH AND MUSCLE FIBER CHARACTERISTICS

By

ANDREA ELIZABETH JANE MILLER, B.A.

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Master of Science

McMaster University

MASTER OF SCIENCE (1990) MCMASTER UNIVERSITY
(Human Biodynamics) Hamilton, Ontario

TITLE: Gender Differences in Strength and Muscle Fiber Characteristics

AUTHOR: Andrea Elizabeth Jane Miller, B.A.
(York University)

SUPERVISOR: Professor J.D. MacDougall

NUMBER OF PAGES: (xvi),145

ABSTRACT

A gender difference in absolute muscle strength is well documented. The extent to which quantitative (fiber area and number) and qualitative (specific tension) differences in muscle contribute to this is not well understood. The purpose of this study was to examine a variety of muscle characteristics in the biceps brachii and vastus lateralis in a sample of males (n=8) and females (n=8) with a wide range of training histories. Measurements included motor unit number, size and activation, and voluntary strength of the elbow flexors and knee extensors. Fiber characteristics were determined from needle biopsies and muscle areas by computerized tomographical scanning. Females were approximately 52% and 66% as strong as the males in the upper and lower body respectively. A significant ($p \leq .05$) correlation was found between strength and muscle cross-sectional area. Females had 45, 41, 30 and 25% smaller muscle cross-sectional areas for the biceps brachii, total elbow flexors, vastus lateralis and total knee extensors respectively ($p \leq .01$). No significant gender difference was found in the strength to cross-sectional area ratio for elbow flexion and knee extension. Males had significantly larger type I fiber areas (4597 vs. 3483 um^2) and mean fiber areas (6632 vs. 3963 um^2) than females in biceps brachii ($p \leq .05$) and significantly larger type II fiber areas (7700 vs. 4040 um2) and mean fiber areas (7070 vs. 4290 um2) in the

vastus lateralis ($p \leq .05$). The difference in type II fiber area in the biceps brachii was not statistically significant despite the fact that these fibers were almost twice as large in the males as in the females (8207 vs. 4306 um^2). No significant gender difference was found in biceps fiber number (180,620 vs.156,872) or muscle area to fiber area ratio in the vastus lateralis (451,468 vs. 465,007). No significant gender differences were found in any of the motor unit characteristics. The results indicate that the primary determinant of the greater muscle strength of males is their larger mean fiber areas which results in greater muscle cross-sectional areas.

ACKNOWLEDGEMENTS

The completion of this thesis would not have been possible without the contributions of a number of individuals. I would first like to thank my supervisor, Dr. Duncan MacDougall for his guidance and support over the past two years. I would also like to express my appreciation to my thesis committee members, Dr. Digby Sale and Dr. Joe Blimkie for their willingness to assist me whenever needed. A special thanks to Dr. Mark Tarnopolsky whose dedication to his field and enthusiasm for every project, big or small, was truly an inspiration to me.

To those individuals who instructed me in the various techniques required to conduct my research, John Moroz, Joan Martin and Doug Oleksuik, I would like to thank-you for your patience. Thanks to both Dr. Jim Dowling and Nick Cardone for their asssistance with the CT scans and to Vicky Galea for her important contribution to my data collection.

A big "thank-you" is extended to Tali Bar-Or for her incredible energy and assistance throughout what was the most chaotic two months of my life.

The encouragement and compassion extended to me over the past two years, both professionally and personally, by my dear friend Allan Chesley will never be forgotten. Thanks to my closest friends Beth Boyd, Lois Kelsey and Darlene Tanasychuk whose love and laughter during a time in which I thought the title of this thesis might end up being "The Height and Weight of a Few People" helped me to keep everything in perspective.

Finally, I want to thank my family for their love and encouragement throughout this and all my endeavours, and Lori Boyce for her patience and support, and her faith in my dreams.

PREFACE

This thesis is somewhat different from the traditional style in that it is presented in two chapters. Chapter 1 is a review of the literature and also presents the rationale for the research project. Chapter 2 is a summary of the study, similar to that which will be submitted for journal publication.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

1.1 INTRODUCTION

Gender differences in absolute muscle strength are well documented (Laubach 1976; Komi & Karlsson 1978). Although males are generally stronger than females, considerable overlap exists between the sexes (Maughan et al. 1986). The gender difference is greater in measurements of upper than lower body strength (Levine et al. 1984; Heyward et al. 1986). A review of nine separate studies examining gender differences in strength found upper extremity values in women ranging from 35 to 79% of men's (average = 56%) and lower extremity values in women ranging from 57 to 86% (average = 72%) (Laubach 1976).

Studies in which strength is normalized to lean body mass report a significant gender difference in relative upper body strength, while no such difference is found in relative lower body strength (Wilmore 1974; Levine et al. 1984). These findings may be indicative of differences in muscle mass distribution between the sexes. In females, the upper limbs represent a smaller proportion of the total body mass than in males, thus, putting them at a disadvantage when upper body strength is reported relative to lean body mass.

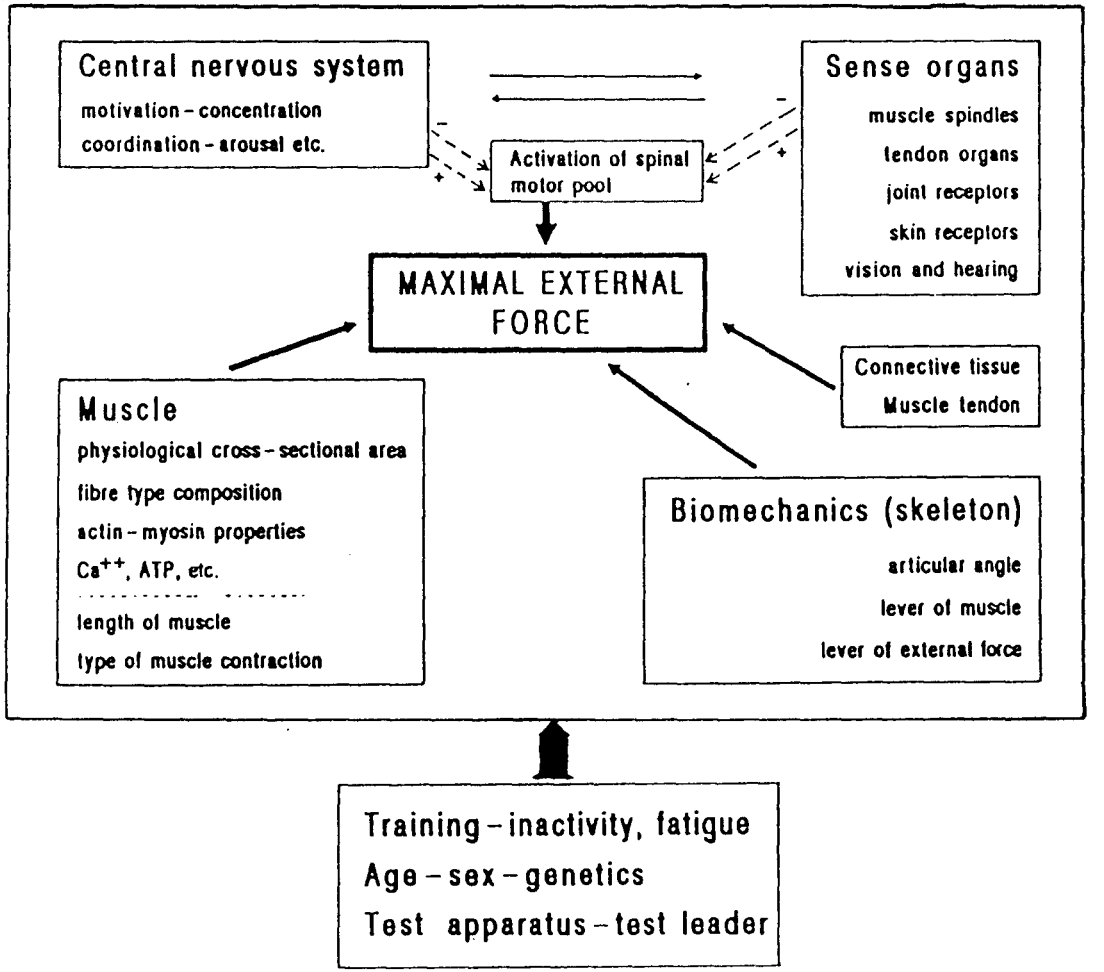
The factors involved in the expression of maximum voluntary strength are illustrated in Figure 1. Factors that may be responsible for the gender difference in absolute strength include: muscle cross-sectional area (CSA), the specific tension of muscle (force per unit muscle CSA), motor unit activation, and the mechanical advantage acting across the joint.

Gender differences in absolute muscle strength, therefore, may be the result of qualitative and/or quantitative differences in male and female muscle tissue in addition to differences in neural activation and the mechanical advantage acting at the joint. The extent to which these differences contribute to the gender difference in absolute strength is the basis of the following discussion.

The evidence for qualitative differences in male and female muscle tissue is equivocal. The finding that strength and muscle cross-sectional area (CSA) are highly correlated (Ikai & Fukunaga 1968; Maughan et al. 1983; Maughan & Nimmo 1984) and that the strength to CSA ratio is similar for males and females (Ikai & Fukunaga 1968; Schantz et al. 1983; Sale et al. 1987) suggests that female muscle tissue does not differ in potential force production from male muscle tissue (Holloway & Baechle 1990). In contrast, a number of investigators have reported that males have a significantly greater strength to CSA ratio than females and

FIGURE 1: FACTORS INVOLVED IN THE EXPRESSION OF MAXIMUM VOLUNTARY STRENGTH

Taken from: K. Klausen's "Strength and Weight Training". In Physiology of Sports T. Reilly, N. Secher, P. Snell, and C. Williams (eds.) E. & F.N. Spon. London: 1990.


Central nervous system
motivation - concentration
coordination - arousal etc.
Activation of spinal motor pool
Sense organs
muscle spindles
tendon organs
joint receptors
skin receptors
vision and hearing
MAXIMAL EXTERNAL FORCE
Muscle
physiological cross - sectional area
fibre type composition
actin - myosin properties
Ca++, ATP, etc.
length of muscle
type of muscle contraction
Connective tissue
Muscle tendon
Biomechanics (skeleton)
articular angle
lever of muscle
lever of external force
Training - inactivity, fatigue
Age - sex - genetics
Test apparatus - test leader

therefore, gender differences in absolute strength may be attributed to factors other than just magnitude of muscle mass (Morris 1948; Young et al. 1985; Ryushi et al. 1988). It is, however, important to note that large inter-individual differences in the strength to CSA ratio have also been observed within each gender, suggesting that the factors responsible for the variability in the ratio may not be gender specific (Maughan et al. 1983; Maughan & Nimmo 1984).

The strength to CSA ratio will be influenced by the specific tension (strength per unit contractile tissue) of the muscle and it has been suggested that the specific tension may be affected by the fiber type distribution (Tesch & Karlsson 1978; Young 1984; Ryushi et al. 1988). This is unlikely considering the finding of a number of investigators that Type I and Type II muscle fibers do not differ in their ability to generate force per unit CSA (Sale et al. 1983; Schantz et al. 1983; Sale et al. 1987). While having little or no effect on the peak force of isometric contractions, the fiber type distribution pattern of a muscle may influence the peak force of concentric contractions, particularly if performed at high velocities (Thorstensson et al. 1976). Thorstensson et al. (1976) found that individuals with high percentages of fast twitch muscle fibers had higher force output during maximal voluntary contractions at high speeds.

Connective tissue is present throughout muscle tissue and is comprised of collagen, elastin and adipose tissue. Connective tissue is non-contractile tissue which serves to support and bind muscle tissue (Van DeGraaff 1984). Studies have shown that female muscle tissue contains proportionately more connective tissue than male muscle (MacDougall et al. 1983; Sale et al. 1987). Gender differences in the proportion of connective tissue present in muscle, therefore, could influence the specific tension and hence, account for some of the variability in the strength to CSA ratios.

Ryushi et al.(1988) suggested that incomplete neural activation in females during a maximal voluntary muscular contraction could, in part, explain the greater strength to CSA ratio reported in males. A motor unit consists of one motor neuron and the aggregation of muscle fibers it innervates. When a motor unit is recruited and firing at optimal frequency all of its muscle fibers will contract maximally. A true maximal voluntary contraction requires that all motor units be recruited. There does not appear, however, to be any evidence to suggest that males are better able to maximally activate their motor units than females (Belanger & McComas 1981; Young et al. 1985). The possibility remains, however, that a gender difference in motor unit number and/or motor unit size may affect recruitment and synchronization patterns which could influence the expression of maximal voluntary strength.

It has been reported that anatomical differences can account for at least part of the variability in the strength to CSA ratio (McCullagh et al. 1984). For example, the dimensions of the levers about the centre of rotation of the knee joint determine the mechanical advantage across the knee joint. A significant positive relationship has been shown to exist between the strength to CSA ratio in the knee extensors and the mechanical advantage across the knee (McCullagh et al. 1984). Males tend to have longer bones and, hence have greater moment arm lengths than females. As a result, males have a greater mechanical advantage than females during muscular contractions.

The greatest determinant of a muscle's strength is it's cross-sectional area (Maughan & Nimmo 1984). Males typically have greater muscle cross-sectional areas and therefore perform better on upper and lower body strength measurement tests. Smaller gender differences in maximum strength have been reported in competitive athletes suggesting habitual rather than genetic dissimilarities between males and females (Fugl-Meyer 1981). A number of investigators, however, have found untrained males to be significantly stronger than both female basketball and volleyball players (Morrow & Hosler 1981) and competitive female bodybuilders (Bond et al. 1985). This latter study, however, found a significant

gender difference only in upper body absolute muscle strength (Bond et al. 1985). These findings indicate that, despite significant increases in the muscle mass of females after intense training, their muscle CSA and hence, strength performance, remains only equal to or inferior to that of the average untrained male.

Muscle CSA is determined by both the size and number of individual muscle fibers. The extent to which fiber size and number contribute to the greater muscle CSA of males is not known. Consequently, the following discussion will examine muscle fiber development and growth. This will be followed by a review of the literature dealing with fiber characteristics of male and female adults, and finally, a rationale will be presented for the present study.

1.2 MUSCLE FIBER DEVELOPMENT AND GROWTH

1.2.1 Myogenesis

Early in embryonic development specialized mesodermal cells begin rapid mitotic division giving rise to millions of mononucleated myoblasts. During the 4th week of gestation these myoblasts align and fuse together to form multinucleated myotubes. As the myotubes mature, the centrally located nuclei migrate to the periphery and further expression of contractile and regulatory proteins occur (White and Esser 1989). While it appears that muscle fiber development is not complete until birth, fetal movements strong enough to be felt by the mother begin to occur by the 17th week of gestation (Van De Graaff 1984). After birth, the peripherally located nuclei within the muscle fibers lose the capacity for mitotic activity and therefore, it is believed that fiber number is established at the time of birth (Van De Graaff 1984). Other investigators, however, have found an increase (Betz et al. 1979) and decrease (Layman et al. 1980) in fiber number in rat muscle tissue shortly after birth.

During myogenesis, it appears that a sub-population of myoblasts do not become incorporated into developing myotubes but remain instead on the surface of the myofiber. These mononucleated satellite cells are present throughout the life of all skeletal myofibers and constitute between 2-10% of the total fiber-associated myonuclei (Schultz 1989; White & Esser 1989). Visually detectable only through an electron microscope, a satellite cell's identifying characteristic is its location outside the muscle plasma membrane but within the basal lamina (White & Esser 1989). The role of satellite cells in post-natal myofiber growth will be discussed later.

No concensus exists as to when the metabolic properties of a muscle fiber are determined. Increases in the percentage of type I fibers postnatally has led to the suggestion that muscle fiber types are not fully differentiated at birth and the process continues throughout the first year of life (Elder 1979). The mechanism(s) responsible for fiber differentiation are not well understood. Muscle tissue grown in culture does not differentiate into distinct fiber types suggesting that control of fiber differentiation is exerted through the nervous system (Jolesz & Sreter 1981), either by impulse activity or by the secretion of "trophic" substances (Elder 1986).

Komi et al.(1977) reported similar fiber type distributions in monozygotic twins while dizygotic twins differed in their

histochemical profiles. This finding suggests a strong genetic influence on muscle fiber composition; however, Bouchard et al. (1985) in a similar study found no significant genetic effect for fiber type distribution. In addition, Fugl-Meyer et al. (1982) found left to right assymetry in the fiber composition of wrist muscles suggesting that fiber compostition may be due, in part, to functional adaptation. Further research is needed to determine the role of genetics in fiber differentiation.

At birth, many fibers exhibit polyneuronal innervation (Gans 1982). The possibility of neuronal competition and its role in the fiber differentiation process has not been rigorously investigated (Purves 1980). It has been suggested that the factors controlling gene expression are responsive to a variety of physiological and environmental stimuli during the early muscle developmental stage which could alter the functional characteristics of the muscle fiber (Baldwin 1984). Therefore, fiber differentiation and growth appears to be the result of both genetic and environmental influences (Gans 1982; Baldwin 1984; Bouchard et al. 1985). Though it has been reported that the fiber type distribution pattern in the skeletal muscle of six year old children is similar to that of normal adult muscle (Bell et al. 1980), the possibility that fiber type conversions during adolescent and adult life might occur cannot be dismissed.

1.2.2. Normal Developmental and Activity-Induced Muscle Growth

The early work of Bigland and Jehring (1952) and Goldberg (1967) demonstrated that two types of muscle growth could be distinguished. The first, normal developmental growth, requires the presence of pituitary growth hormone. Following hypophysectomy in rats, muscle growth stops, only to resume when growth hormone treatment is initiated (Bigland & Jehring 1952). The second type of muscle growth, activity-induced growth, does not require growth hormone (Goldberg 1967). This growth occurs in response to increased functional demands on the muscle although the mechanisms for such growth have not yet been elucidated.

1.2.3. Normal Developmental Growth of Myofibers

Post-natal muscle fiber growth is accomplished by increases in both the area and length of the myofibers (Aherne et al. 1971). The increase in length is due to the addition of sarcomeres in series within the myofibril and not the result of an increase in average sarcomere length (Close 1972). Increases in myofiber area are achieved by an increase in the number of myofibrils, which is thought to result from the longitudinal splitting of individual myofibrils, as well as an increase in myofibril cross-sectional area (Goldspink 1970). In addition, growth is facilitated by the division of satellite cells and the subsequent fusion of one or both daughter

cells into the myofiber. By doing so satellite cells contribute additional nuclei and small amounts of cytoplasm to the maturing post-mitotic myofiber thereby maintaining a constant myonuclei (DNA) to cytoplasmic ratio (Schultz 1989; White & Esser 1989). Though not completely understood, there is increasing evidence that insulin-like growth factors, somatomedins, are capable of mediating the actions of growth hormone in muscle by the stimulation and inhibition of satellite cell proliferation (Florini 1987; White & Esser 1989). Following the immediate post-natal period the relative number of satellite cells in all muscles rapidly decreases and continues to decrease, though at a slower rate, throughout life. (Schultz 1989; White & Esser 1989).

A steady increase in fiber size is found with increasing body size in infants, children and adolescents (Aherne et al. 1971). Brooke and Engel (1969b) found that there was no significant difference between human male and female muscle tissue as to fiber types or fiber size during the first decade of life. Additional information regarding fiber characteristics in children is scarce due to ethical considerations which limit in vivo measurement. Those studies which have been done were carried out on muscle tissue obtained post-mortem or from individuals suffering from a variety of neuromuscular diseases (Aherne et al. 1971). As a result, the number of subjects in each age category is small, thereby making fiber

comparisons in children inconclusive. It appears, however, that the rate of growth of muscle fibers during childhood is similar for males and females.

During the adolescent growth spurt the level of circulating testosterone increases dramatically in males. On average, adult males have 10 to 15 times the level of circulating testosterone as adult females. Such increases are said to be responsible for the greater muscle mass of males compared to females (Brown & Wilmore 1974; Fahey et al. 1976), however the role of testosterone in muscle fiber growth is not well understood. It has been suggested that "the androgen participates in the growth spurt during adolescence by enhancing the somatomedin effect and/or potentiating the production of somatomedin by growth hormone" (Kawai et al. 1982 as cited in Florini 1987). While the mechanism by which testosterone promotes muscle growth has not been fully elucidated, it appears that this androgen is involved in the greater growth rate of muscle fibers observed in males during adolescence. Support for this suggestion comes from the findings of a recent study which found that a pharmacological dose of testosterone enanthate given over 12 weeks increased muscle mass by increasing muscle protein synthesis in normal male subjects in the absence of an additional exercise stimulus (Griggs et al. 1989).

Testosterone may have an indirect influence on muscle growth since this androgen is known to promote aggressive behaviour in males (Pope & Katz 1988). Males with higher testosterone levels who participate in sporting activities and training, may do so more aggressively, thus enhancing muscle hypertrophy and making it difficult to distinguish normal developmental from activity-induced muscle growth in young males.

1.2.4 Activity-Induced Muscle Growth

The mechanism(s) responsible for skeletal muscle hypertrophy in response to increased functional demands are not well understood. While growth hormone is required for normal developmental growth, activity-induced muscle growth can occur in hypophysectomized animals (Goldberg 1967). Goldberg's work with hypophysectomized rats also implies that testosterone, thyroid hormone and insulin are not required for activity-induced muscle growth (Goldberg et al. 1975). While still controversial, the initial stimulus for this type of muscle growth appears to come from the stretch, tension or some other mechanical distortion produced in the muscle during forceful contraction (Goldberg et al. 1975).

It has traditionally been thought that skeletal muscle fiber number is established at birth and that muscle growth is achieved by enlargement of existing fibers (Goldberg et al. 1975; Van De Graaf

1984). A number of investigators, however, have reported an increased fiber number in response to increased functional demands in a variety of animal models (Hall-Craggs 1970; Gonyea et al. 1977; Ho et al. 1980). One of these authors cautions that the longitudinal division of fibers observed was limited and frequently associated with degeneration of portions of the fiber (Hall-Craggs 1970). It could therefore be argued that fiber splitting is not part of the uniform histological process leading to muscle hypertrohpy but is the result of injury to individual fibers (Hall-Craggs 1970). This suggestion is supported by the finding of Gollnick et al. (1981) that fiber number did not increase in the functionally overloaded skeletal muscle of rats. The possibility also exists for satellite cell activation to lead to fiber hyperplasia if the training stimulus is severe (White & Esser 1989). Differences in the methods used to count fibers, the muscles examined and the training protocols may explain the conflicting results in regards to changes in fiber number. It appears that skeletal muscle possesses the capacity for both hypertrophy and hyperplasia (White & Esser 1989). More work needs to be done to determine if new fibres are formed to replace previous fibres or if de novo synthesis occurs (White & Esser 1989).

A. The role of satellite cells in activity-induced muscle growth. The role of satellite cells in activity induced muscle growth has not been defined. The absence of satellite cells in cardiac muscle, a tissue capable of hypertrophy in response to

increases in functional demand, indicates their role is not an obligatory one (White & Esser 1989). Similar to normal developmental muscle growth, maintenance of a constant DNA to cytoplasmic ratio by division and subsequent fusion of satellite cells has been suggested for models of activity-induced muscle growth (White & Esser 1989). Some evidence suggests the involvement of growth factors in the regulation of satellite cell activity in response to an exercise stimulus (Yamada et al. 1989). Until the mechanism(s) responsible for satellite cell activation and regulation are fully elucidated their role in activity-induced muscle growth remains speculative.

B. Activity-induced muscle growth in males and females.

Despite Goldberg's (1967) findings that testosterone is not required for activity-induced muscle hypertrophy, a number of investigators have reported a significantly greater degree of muscle hypertrophy following weight-training in males than in females, and have attributed this difference to males' higher level of circulating testosterone (Mayhew & Gross 1974; Wilmore 1974; Krahenbuhl et al. 1978). While testosterone may not be required for activity-induced hypertrophy, its involvement in skeletal muscle growth during the adolescent growth spurt in males suggests it may enhance the activity-induced process (Griggs et al. 1989). In contrast, a number of studies have found no relationship between the levels of blood androgens and the extent of muscle hypertrophy in males and females

(Hetrick & Wilmore 1979; Westerlind et al. 1987). Females are capable of significant gains in muscle mass in response to weight-training despite relatively low levels of circulating testosterone (Cureton et al. 1988). Kuhn and Max (1985) found testosterone did not enhance the hypertrophy process in female rats. The possibility remains that other naturally occurring hormones may have a potent anabolic effect in female muscle tissue similar to that of testosterone's alleged effect in males (Wilson 1972; Krahenbul et al. 1978).

1.3 GENDER DIFFERENCES IN MUSCLE FIBER CHARACTERISTICS

1.3.1 Fiber Type Distribution

In addition to those studies which have examined fiber type distribution patterns in untrained males and females, a number of studies have included competitive athletes and trained bodybuilders in their subject populations (Costill et al. 1976; MacDougall et al. 1982; Sale et al. 1987). Costill et al. (1976) reported similar fiber type distributions in the gastrocnemius muscle of male (50.2 % slow-twitch fibers (ST)) and female (50.2 % ST) track athletes and untrained men (52.6% ST) and women (51.0% ST). Not surprisingly, when the athletes were divided on the basis of their event, distance runners (male and female) were found to have a significantly larger percentage of slow-twitch fibers (Costill et al. 1976). MacDougall et al. (1982) reported similar fiber type distributions in the biceps brachii of elite powerlifters, bodybuilders and trained controls. Similarily, Sale et al. (1987) found no significant difference in fiber type distribution in the biceps of male bodybuilders, untrained males and females. Other investigators have reported similar fiber type distribution patterns in the tibialis anterior of untrained males and females (Henriksson-Larsen 1985), the biceps brachii of male and female bodybuilders (Alway et al. 1989), and the vastus

lateralis of untrained males and females (Prince et al. 1977). In contrast, Komi and Karlsson (1978) found male vastus lateralis contained a higher percentage of slow-twitch fibers (55.9%) than comparable female muscle tissue (49.1%). Another investigator, however, found the percentage of ST fibers in male vastus lateralis (36.9%) to be significantly lower than in females (42.7%) (Simoneau et al. 1985). A large study conducted by Simoneau and Bouchard (1989) in which a total of 418 muscle biopsies from the vastus lateralis of both sexes were examined, found that males had a lower percentage of ST fibers in this muscle than females.

While gender differences in fiber type distribution are intriquing, they cannot fully explain the greater muscle CSA and strength observed in males.

1.3.2 Fiber Size

Brooke and Engel (1969) first reported that type II (fast-twitch) fibers in males are larger than the type I (slow-twitch) fibers, but that the reverse is true in females (I > II). Edstrom and Nystrom (1969) found that females have smaller type I and type II muscle fibers than males although the size difference was more pronounced in the type II fibers.

In more recent studies, a gender difference in mean fiber area has been demonstrated. Males have a greater mean fiber area in the biceps brachii (MacDougall et al. 1983; Sale et al. 1987) and the

tibialis anterior (Henriksson-Larsen 1985). Female athletes have larger type I and type II muscle fibers in the gastrocnemius (Costill et al. 1976) and vastus lateralis (Prince et al. 1977) than untrained females, but significantly smaller fibers than male athletes (Costill et al. 1976). A similar gender difference in fiber size has been reported for the biceps brachii of male and female bodybuilders (Alway et al. 1989).

In contrast to the findings of Brooke and Engel (1969), many investigators have found that while type II fibers are larger than type I fibers in males, the reverse is not always found in females (Costill et al. 1976; Bell & Jacobs 1989) In the latter study, type I and type II muscle fibers of the vastus lateralis were found to be similar in size in female bodybuilders (Bell & Jacobs 1989). Costill et al. (1976) found the type II fibers to be larger than the type I fibers in the gastrocnemius of female track athletes. In both these studies, however, the subjects were considered to be well-trained, lending support to Brooke and Engel's (1969a) suggestion that the larger type II fibers in males results from their greater involvement in activities which place a high emphasis on strength, thereby developing these fibers. Therefore, the size difference between type I and type II fibers may be the result of differences in training status rather than dependent upon gender.

1.3.3 Fiber Number

The results of studies examining fiber number in male and female muscle tissue have been equivocal. Schantz et al.(1983) found no gender difference in fiber number in the triceps brachii. This finding is similar to that of their earlier research in which they reported that males and females had similar fiber numbers in the vastus lateralis, despite large differences in thigh girth (Schantz et al. 1981). In both these studies, however, no correction was made to the total muscle CSA for connective tissue. Failure to correct muscle CSA for the amount of connective tissue present results in the overestimation of fiber number. In addition, the vastus lateralis is a pennate muscle such that the fibers do not run parallel to the line of action, therefore the physiological CSA and the anatomical CSA of this muscle are not the same (Gollnick et al. 1981; Davies et al. 1988; Narici et al. 1989). The estimation method used by Schantz et al. (1981) to determine fiber number in the vastus lateralis is invalid because it assumes that the physiological CSA and the anatomical CSA are similar.

Studies which have corrected for the amount of connective tissue present in muscle offer conflicting results (MacDougall et al. 1983; Sale et al. 1987; Alway et al. 1989). Alway et al. (1989) failed to observe a significant gender difference in fiber number in the biceps brachii of male and female bodybuilders. In studies

involving untrained subjects, females were found to have significantly fewer muscle fibers in the biceps brachii (MacDougall et al. 1983; Sale et al. 1987). A similar gender difference in fiber number was observed in the tibialis anterior (Henriksson-Larsen 1985).

1.4 RATIONALE FOR THE PRESENT STUDY

Strength differences between the sexes are well documented (Laubach 1976). These differences may be the result of qualitative and/or quantitative differences in male and female muscle tissue, in addition to differences in motor unit characteristics and the mechanical advantage acting across the joint.

A number of investigators have reported that the strength/CSA ratio is greater in males than in females (Morris 1948; Young et al. 1985; Ryushi et al. 1988), however, considerable variation exists within each gender (Maughan et al. 1983; Maughan & Nimmo). Differences in limb lengths (McCullagh et al. 1984) and the connective tissue volume density (Sale et al. 1987) probably account for some of the variability in the strength/CSA ratio between and within genders.

The factor considered to be primarily responsible for the greater absolute strength of males is their larger muscle CSA (Maughan et al. 1984). While studies have consistently demonstrated the existence of a gender difference in muscle fiber size (Edstom & Nystrom 1969; MacDougall et al. 1983; Sale et al. 1987), the contribution of differences in fiber number to the greater muscle CSA

of males is not well understood and warrants additional study. The larger muscle fibers in males may result from differences in physical activity patterns (behavioral) or hormonal influences (biological) or a combination of both. A gender difference in fiber number, however, would appear to be the result of biological/genetic influences since it has traditionally been believed that fiber number is determined at birth and that evidence to support the role of hyperplasia in skeletal muscle growth is scarce. If a gender difference in fiber number is found to exist, males would appear to have a "genetic advantage" in terms of skeletal muscle growth, regardless of fiber area.

CHAPTER 2

2.1 INTRODUCTION

Gender differences in absolute muscle strength are well documented (Laubach 1976). Although males are generally stronger than females, considerable overlap exists between the sexes (Maughan et al. 1986). This difference has been shown to be greater in measurements of upper than lower body strength (Levine et al. 1984; Heyward et al. 1986).

Factors which may explain the gender difference in maximum voluntary strength include: muscle cross-sectional area (CSA), specific tension of muscle (the force per unit CSA, which may be influenced by fiber type distribution and connective tissue volume density), motor unit activation and the mechanical advantage acting across the joint.

Strength and muscle CSA are positively correlated (Ikai & Fukunaga 1968; Maughan et al. 1983; Maughan & Nimmo 1984), and many investigators have found that the strength to muscle CSA ratio is similar for males and females. A number of studies, however, have found that males have a significantly greater strength to muscle CSA

(Morris 1948; Young et al. 1985; Ryushi et al. 1988). This would suggest that male muscle tissue has a greater ability to generate force than female muscle tissue. Large inter-individual differences in the strength to CSA ratio are also found within each gender, however, suggesting that the factors responsible for the variability in the ratio may not be gender specific (Maughan et al. 1983; Maughan & Nimmo 1984).

It is unlikely that the variability observed in the strength to CSA ratio results from differences in either fiber type distribution (Schantz et al. 1983; Sale et al. 1987) or motor unit activation (Belanger & McComas 1981; Young et al. 1985). Anatomical differences which affect the mechanical advantage acting across a joint could account for some of the observed variability in the strength to CSA ratio (McCullagh et al. 1984) as might the greater proportion of connective tissue (non-contractile) found in female muscle (Sale et al. 1987).

The greatest determinant of a muscle's strength is its size (Maughan & Nimmo 1984). Muscle CSA is determined by both the size and number of muscle fibers. The extent to which fiber size and number contribute to the greater muscle CSA observed in males is unknown.

A gender difference in fiber size has consistently been demonstrated. Normal males have a significantly larger mean fiber area than females in the biceps brachii (MacDougall et al. 1983; Sale et al. 1987), and the tibialis anterior (Henriksson-Larsen 1985). Female athletes have larger type I and type II muscle fibers in the gastrocnemius than untrained females, however their mean fiber size remains significantly smaller than in male athletes (Costill et al. 1976).

The results of studies examining fiber number in male and female muscle tissue have been equivocal. Schantz et al. (1981,1983) reported similar fiber numbers in males and females in both the triceps brachii and vastus lateralis. The failure of these investigators, however, to correct muscle CSA for the amount of connective tissue present may have affected the validity of their findings. Other studies which have corrected for connective tissue offer conflicting results. Alway et al. (1989) found no significant gender difference in fiber number in the biceps brachii of male and female bodybuilders. In contrast, untrained females were found to have significantly fewer muscle fibers in the biceps brachii (MacDougall et al. 1983; Sale et al. 1987) and the tibialis anterior (Henriksson-Larsen 1985).

The purpose of the present study was to examine a variety of muscle fiber characteristics in a sample of males and females with a wide range of training histories, so that the contributions of fiber area, number and distribution to the greater CSA and strength of males could be determined. A gender difference in muscle fiber size may result from behavioural (physical activity patterns) or biological differences (hormonal influence) or a combination of both. A gender difference in fiber number would appear to be the result of biological differences since it has traditionally been believed that fiber number is determined at birth (Van DeGraaff 1984). A significant gender difference in fiber number would suggest that males have a "genetic advantage" in terms of skeletal muscle growth. Since gender differences in strength are reported to be greater in the muscles of the upper body, it was considered important to include a muscle of the arm (biceps brachii) as well as the thigh (vastus lateralis).

A measurement of motor unit number, size and activation was done to determine the influence of these parameters on the gender difference in maximum voluntary strength.

A secondary purpose of this study was to examine muscular endurance in both upper and lower body muscle groups in the same study sample to determine if a gender difference exists.

2.2 METHODS

2.2.1 Subjects

Eight males and eight females served as subjects. Their physical characteristics are presented in Table 1. An effort was made to recruit subjects of both sexes who displayed a wide range in muscle size and training histories (Table 2). All subjects were aware of the purpose and risks associated with the study and gave informed written consent. All measurements were performed in accordance with the policies of the McMaster University Committee on The Ethics of Research on Human Subjects (Appendix III).

2.2.2 Body Density

Body density was determined by hydrostatic weighing and residual lung volume measured using the closed circuit helium dilution method (Motley 1957). Each subject was given 4 underwater weighing trials. The average body density was then used to calculate percent body fat using the equation of Brozek et al. (1963). Lean body mass was calculated by subtracting fat weight from total body weight.

Table 1. Subjects' Physical Characteristics

Sub.	Age	Sex	Height (cm)	Weight (kg)	%Body Fat	LBM (kg)	Femur Length (cm)	Tot.Arm Length (cm)
JS	21	F	157.5	52.3	25.7	38.9	35.5	50.5
CH	23	F	165.7	83.3	34.3	54.7	37.5	55.0
LB	31	F	168.9	70.6	20.4	56.1	38.0	52.2
CM	24	F	175.9	71.5	21.9	55.8	42.2	54.9
DS	26	F	160.7	52.7	10.1	47.4	35.8	51.9
KA	22	F	161.9	55.9	22.4	43.4	40.2	48.9
NJ	22	F	168.9	61.2	19.7	49.1	43.6	55.9
SL	31	F	166.5	67.9	25.0	50.9	42.0	53.0
MEAN	25.0 ±1.4		165.8 ±2.0	64.4 ±3.8	22.4 ±2.4	49.5 ±2.2	39.4 ±1.1	52.5 ±.92
GP	23	M	177.8	78.9	18.8	64.1	43.5	58.2
JK	19	M	170.0	65.1	6.8	60.7	40.6	53.7
JC	21	M	175.3	77.4	14.2	66.4	41.0	58.4
AC	26	M	170.8	82.0	23.5	62.7	41.0	54.7
YW	27	M	187.0	69.2	12.7	60.4	39.0	59.1
XS	29	M	172.5	60.1	14.3	51.5	36.1	55.6
JW	21	M	178.5	78.0	7.8	71.9	36.0	58.1
JB	20	M	183.5	83.6	8.9	75.6	41.0	58.4
MEAN	23.3 ±1.3		176.9★ ± 2.1	74.3 ±3.0	13.4★ ± 2.0	64.2★ ± 2.6	39.8 ±.9	57.0★ ±.7

Values are means ± SE
★$p \leq 0.01$ for differences between female and male groups

Table 2. Subjects' Training Histories

Subject	Immediate Training History (2 months prior to study) (times/week)	Total Training History (3 years prior to study) (times/week)
Females		
JS	3	2-3
CH	0	0
LB	0	0
CM	2-3	2-3
DS	3	0
KA	1-2	6
NJ	3	3
SL	4	4
Males		
GP	4	0
JK	6	6
JC	0	0
AC	4	4-6
YW	0	0
JW	4	4
JB	5	5

2.2.3 Bone Lengths

Limb lengths for each subject were recorded so that the effects of differences in lever-arm length could be considered in interpreting strength measurements. The length of the radius and humerus were measured using techniques previously described (Cameron 1978). Briefly, radius length was measured from the head of the radius at the elbow to the styloid process at the wrist. Humerus length was measured from the laterosuperior margin of the head of the radius to the lateral border of the acromion process. Femur length was measured from the greater trochanter to the lateral condyle of the tibia.

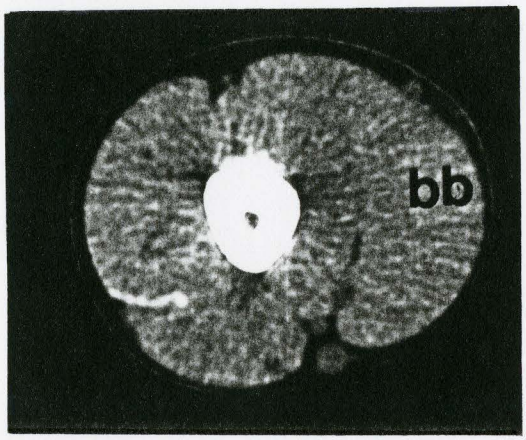
2.2.4 Muscle Cross-Sectional Area

Cross-sectional area (CSA) of the right biceps brachii and the right vastus lateralis was determined from computerized tomography scans (Ohio Nuclear, model 20/20). The biceps brachii was scanned with the elbow extended, at a level corresponding to 75% of the distance from the tip of the acromion process of the scapula to the medial epicondyle of the humerus (Figure 2a). The vastus lateralis muscle was scanned at the mid-thigh level, which was taken as the mid-point between the greater trochanter and the lateral condyle of the tibia (Figure 2b). Muscle areas were measured by a custom-made computerized digitizer using the Sigmascan software

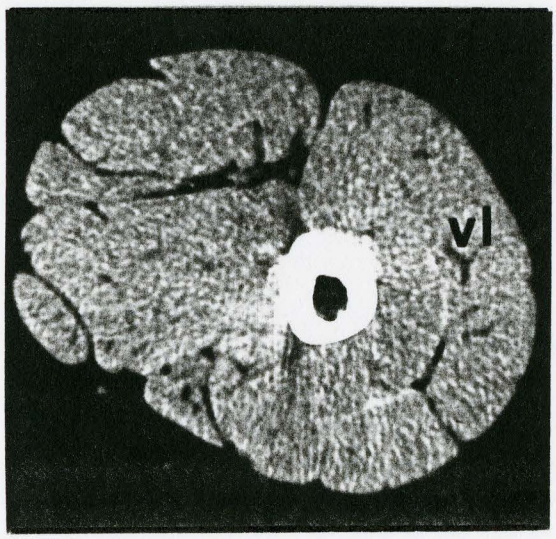
FIGURE 2: A. COMPUTERIZED TOMOGRAPHIC SCAN OF UPPER ARM WITH ELBOW EXTENDED ILLUSTRATING THE BICEPS BRACHII

B. COMPUTERIZED TOMOGRAPHIC SCAN OF THIGH ILLUSTRATING VASTUS LATERALIS

A



B



package (Jandel Scientific, California). From the CT scans used for measurement of biceps brachii and vastus lateralis area, the CSA of the total elbow flexors (biceps plus brachialis) and total knee extensors (quadriceps group) was also determined.

2.2.5 Muscle Fiber Characteristics

Muscle tissue samples were obtained from the biceps brachii and vastus lateralis using the needle biopsy technique. The biopsy sample was mounted cross-sectionally in embedding medium using a stereo microscope and then frozen in isopentane cooled in liquid nitrogen. The tissue was sectioned (10um thick) on a cryostat and separate sections were stained for myofibrillar ATPase (Padykula & Herman 1955) and for collagen and other non-contractile tissue using a modified Gomori trichrome stain (Gomori 1950). Despite preincubation at pH 4.6, most sections allowed only clear differentiation of the Type I and Type II fibers. For this reason the fiber type distributions and fiber areas include only these two fiber types with no subclassification of the Type II fibers.

Tissue sections were photographed under the light microscope and measurements were made on projected slides. Cross-sectional area for type I and type II fibers was measured by a custom-made computerized digitizer for an average of 140 fibers of each type per biopsy. Percent fiber type distribution was estimated by counting an average of 278 fibers/biopsy. The proportion of collagen and other

non-contractile tissue, expressed as a percentage of the muscle CSA, was calculated in the trichrome-stained sections by means of a 168 point, point-counting technique (Weibel 1971). Mean fiber area was calculated to correct for fiber distribution as follows: Fa = (% type I)(mean type I area) + (% type II)(mean type II area)/100. Since most fibers in the biceps brachii are thought to extend from origin to insertion (Davies et al. 1988), fiber number was estimated by dividing the mean fiber area into the biceps cross-sectional area (corrected for connective tissue). Due to technical problems associated with small tissue samples, the proportion of connective tissue in the biceps could not be accurately determined for two of the female and one of the male subjects. The mean percentage of connective tissue for the appropriate gender was therefore used in correcting muscle CSA. In the vastus lateralis the muscle area to fiber area ratio was also calculated in this manner. True fiber number can not be estimated due to the pennate structure of this muscle (Gollnick et al. 1981).

2.2.6 Maximum Isotonic Strength

Maximum isotonic strength (1 RM) of the elbow flexors of the dominant arm was determined using a custom-made elbow flexion apparatus. The seat of this apparatus was adjusted so that the subject's upper arm was horizontal. The handle of the device was grasped with the forearm supinated. The subjects were instructed to

perform a single elbow flexion starting with the elbow fully extended. The lift was considered successful if the subject could bring the weight up to 90 degrees of elbow flexion. Additional weight was added until the subject could not successfully complete the lift. Three minute rest periods were given between lift attempts.

Maximum isotonic strength of the right knee extensors was determined using a Global Gym knee extension apparatus. Subjects started the lift at a knee joint angle of 90 degrees. A successful lift required that the subject fully extend the knee. In order to determine full knee extension, the left leg remained fully extended throughout the lift attempt to serve as a comparison. Additional weight was added until the subject could not successfully complete the lift.

Gradations for loading the apparatus for both elbow flexion and knee extension measurements were to the nearest 0.25 kg. No more than five attempts were needed to determine the maximum lift.

2.2.7 Maximal Voluntary Isometric Contraction

For measurement of the maximal voluntary isometric contraction (MVC) of the dominant arm elbow flexors subjects sat in an adjustable chair with their arm in a custom-made dynamometer. This procedure has been described in detail previously (Blimkie et

al. 1989). Maximal voluntary isometric strength of the arm was measured at 110 degrees of elbow flexion (full extension = 180 degrees).

For measurement of the maximal voluntary isometric contraction of the right knee extensors, the subjects sat on an adjustable bench with their right leg in a custom-made dynamometer. The backrest was adjusted so that both the subject's hip and knee were flexed at an angle of 90 degrees. Subjects were secured to the bench by two large straps, one crossing the hips and the second crossing the thigh. The lower leg was strapped to the support plate of the dynamometer.

For both the arm and leg torque measurements, force was transmitted via straps over the distal and proximal ends of the secured limb to a strain gauge located at the rotational center of the dynamometer. The signal was simultaneously read on-line by computer at a sampling rate of 500 Hz. Subjects were given three trials for both elbow flexion and knee extension. The best trial for each condition was selected for statistical analysis.

2.2.8 Resting Twitch Torque

Resting twitch torque for the dominant arm elbow flexors was measured at the same joint angle and with the same dynamometer as for

voluntary isometric strength. This procedure has been described in detail previously (Blimkie et al. 1989).

Resting twitch torque for the right knee extensors was also measured at the same joint angle and with the same dynamometer as for voluntary isometric strength. The procedure was similar to that described for the elbow flexors (Blimkie et al. 1989) except that the stimuli were delivered to the femoral nerve. Resting twitch torque was determined prior to the MVC trials to avoid the effect of potentiation.

2.2.9 Motor Unit Activation

Motor unit activation of the elbow flexors and the knee extensors were determined using the interpolated twitch technique (Merton 1954). During a true maximal voluntary contraction all the available motor units are firing maximally, therefore no increase in torque can be evoked when a superimposed maximal twitch stimulus is delivered. If the contraction is submaximal, whereby all the available motor units are not being activated, the superimposed maximal twitch stimulus will result in an momentary increase in torque (interpolated twitch) while the stimulus is being delivered. The maximum resting twitch torque (RTT) and the interpolated twitch torque (ITT) can be used to calculate the motor unit activation (MUA) by substituting the value of each into the following equation:

$$MUA = \frac{RTT - ITT}{RTT} \times 100$$

The interpolated twitch technique was executed during the three MVC trials for both the elbow flexors and the knee extensors. The trials producing the highest MUA for both muscle groups was selected for statistical analysis.

2.2.10 Motor Unit Number Estimation

Estimations of motor unit number for both the biceps brachii and vastus medialis were conducted using an automated estimation technique developed by the Departments of Medicine and Biomedical Sciences at McMaster University. This method has yet to be used to estimate motor unit number in the vastus lateralis therefore a estimation could only be done for the vastus medialis and biceps brachii. This technique which has been described in detail previously (Galea et al. 1990) is routinely used in diagnostic EMG at McMaster/Chedoke Hospital in Hamilton, Ontario. The system is totally automated and both the motor nerve stimulation and the analysis of evoked motor unit potentials are computer controlled. The coefficient of variation for estimates "within sessions" has been reported to range from 14 to 26% depending on the muscle examined, with the

overall coefficient of variation being 22.0% (Galea et al. 1990). For estimates "between sessions" the overall coefficient of variation has been reported to be 23.8% (Galea et al. 1990).

2.2.11 Muscular Endurance

The same devices used to determine maximum isotonic stength were used to measure muscular endurance of the elbow flexors and knee extensors. Subjects were required to perform the maximum number of repetitions possible for both elbow flexion and knee extension at a cadence of 10 repetitions per minute. A metronome was used to assist the subjects in maintaining the cadence. A successful lift was determined using similar criteria outlined for maximum isotonic strength. The test was stopped when the subject could no longer maintain the cadence. Muscular endurance of the elbow flexors was measured at a load corresponding to 60% of the elbow flexors 1RM and muscular endurance of the knee extensors was measured at loads corresponding to 40 and 60% of the knee extensors 1RM.

2.2.12 Testing Schedule

The entire testing protocol was conducted over 4 separate days:

Day 1	Day 2	Day 3	Day 4
height	motor unit counting	CT scan	biopsies
weight		endurance	
bone lengths			
MVCs			
body density			
1RM's			

2.2.13 Statistical Analysis

Gender comparisons were made using a 1 factor, between subjects analysis of variance (Practical Statistics, Canadian Academic Technology Inc.) In addition, for many of the parameters, male and female data was pooled and subjected to a correlational analysis. The significance level was set at $p = 0.05$.

2.3 RESULTS

2.3.1. Anthropometric Measurements

The subjects' physical characteristics are presented in Table 1.

A. Height and weight. The males were significantly taller than the females (176.9 cm $\pm$ 2.1 SEM vs. 165.8 cm $\pm$ 2.0 SEM, $p \leq 0.01$). No significant gender difference in body weight was found.

B. Lean body mass. Lean body mass was significantly greater in the males than the females (64.2 kg $\pm$ 2.6 vs. 49.5 kg $\pm$ 2.2, $p \leq 0.01$).

C. Limb lengths. No significant difference was found between the sexes for femur length. Males had significantly greater total arm (humerus + radius) lengths than the females (57.0 cm $\pm$ .7 vs. 52.5 cm $\pm$ .9, $p \leq 0.01$)

2.3.2 Voluntary Strength

Gender differences in voluntary strength are illustrated in

Figures 3B and 3C. Males were significantly stronger for measurements of upper and lower body strength ($p \leq 0.01$). Lower body strength in the females was 62% and 69% of the males for knee extension 1RM and MVC respectively. In measurements of upper body strength, the females were 52% as strong as the males for both elbow flexion MVC and 1RM.

A significant postitive correlation was found between lean body mass and both measures of upper (MVC r=.86/1RM r=.83, $p \leq 0.01$) (Figures 4A and 4B) and lower (MVC r=.67/1RM r=.88, $p \leq 0.01$) body strength (Figure 4C and 4D). When expressed relative to lean body mass, the males also had significantly greater upper and lower body strength ($p \leq 0.05$) (Figure 5D). When strength was expressed relative to lean body mass, the females were 70% and 80% as strong as the males in the upper and lower body respectively.

2.3.3 Evoked Twitch Torque

Gender differences in evoked twitch torque are presented in Figure 3A. No gender difference in knee extensor twitch torque was found. A significant difference in twitch torque was found between the elbow flexors of males (9.5 Nm $\pm$ 1.0) and females (4.6 Nm $\pm$ .5) ($p \leq 0.01$).

FIGURE 3: A. EVOKED TWITCH TORQUE OF THE ELBOW FLEXORS AND KNEE EXTENSORS

n = 8 for females, 8 for males
Values are means ± SE
* $p \leq 0.01$ for differences between female and male groups

B. MAXIMUM VOLUNTARY CONTRACTION OF THE ELBOW FLEXORS AND KNEE EXTENSORS

n = 8 for females, 8 for males
Values are means ± SE
* $p \leq 0.01$ for differences between female and male groups

C. 1 REPETITION MAXIMUM OF THE ELBOW FLEXORS AND KNEE EXTENSORS

n = 8 for females, 8 for males
Values are means ± SE
* $p \leq 0.01$ for differences between female and male groups

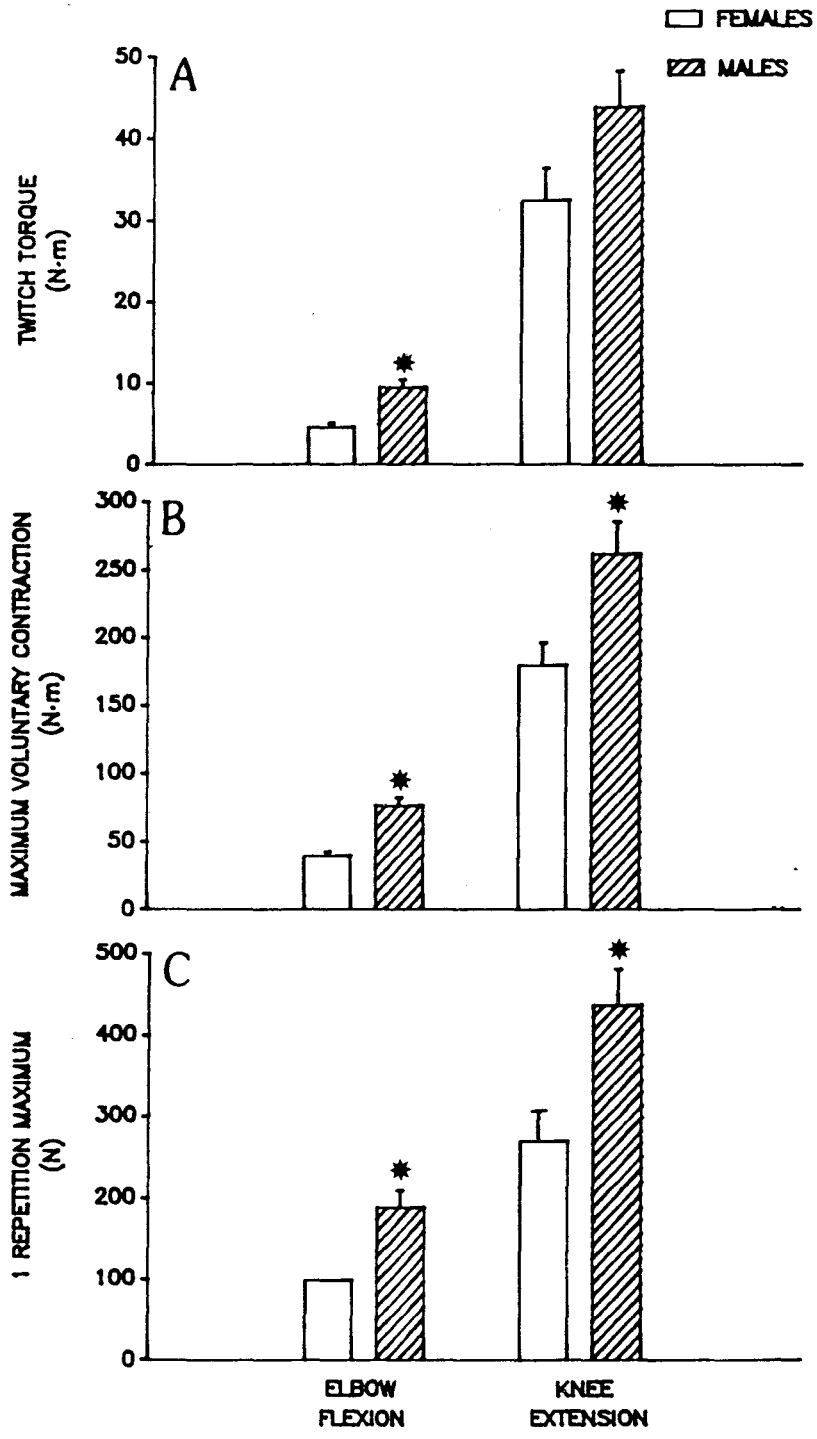

FEMALES
MALES
A
B
C
TWITCH TORQUE (N·m)
MAXIMUM VOLUNTARY CONTRACTION (N·m)
1 REPETITION MAXIMUM (N)
0
10
20
30
40
50
100
150
200
250
300
400
500
ELBOW FLEXION
KNEE EXTENSION

FIGURE 4: A. CORRELATION OF LEAN BODY MASS AND THE 1 REPETITION MAXIMUM OF THE ELBOW FLEXORS

$n = 8$ for females, 8 for males
$r = .83$ ($p \leq 0.01$)
$y = .52(x) - 14.9$

B. CORRELATION OF LEAN BODY MASS AND THE MAXIMUM VOLUNTARY CONTRACTION OF THE ELBOW FLEXORS

$n = 8$ for females, 8 for males
$r = .86$ ($p \leq 0.01$)
$y = 2.0(x) - 56.6$

C. CORRELATION OF LEAN BODY MASS AND THE 1 REPETITION MAXIMUM OF THE KNEE EXTENSORS

$n = 8$ for females, 8 for males
$r = .88$ ($p \leq 0.01$)
$y = 1.2(x) - 30.3$

D. CORRELATION OF LEAN BODY MASS AND THE MAXIMUM VOLUNTARY CONTRACTION OF THE KNEE EXTENSORS

$n = 8$ for females, 8 for males
$r = .67$ ($p \leq 0.01$)
$y = 4.6(x) - 42.2$

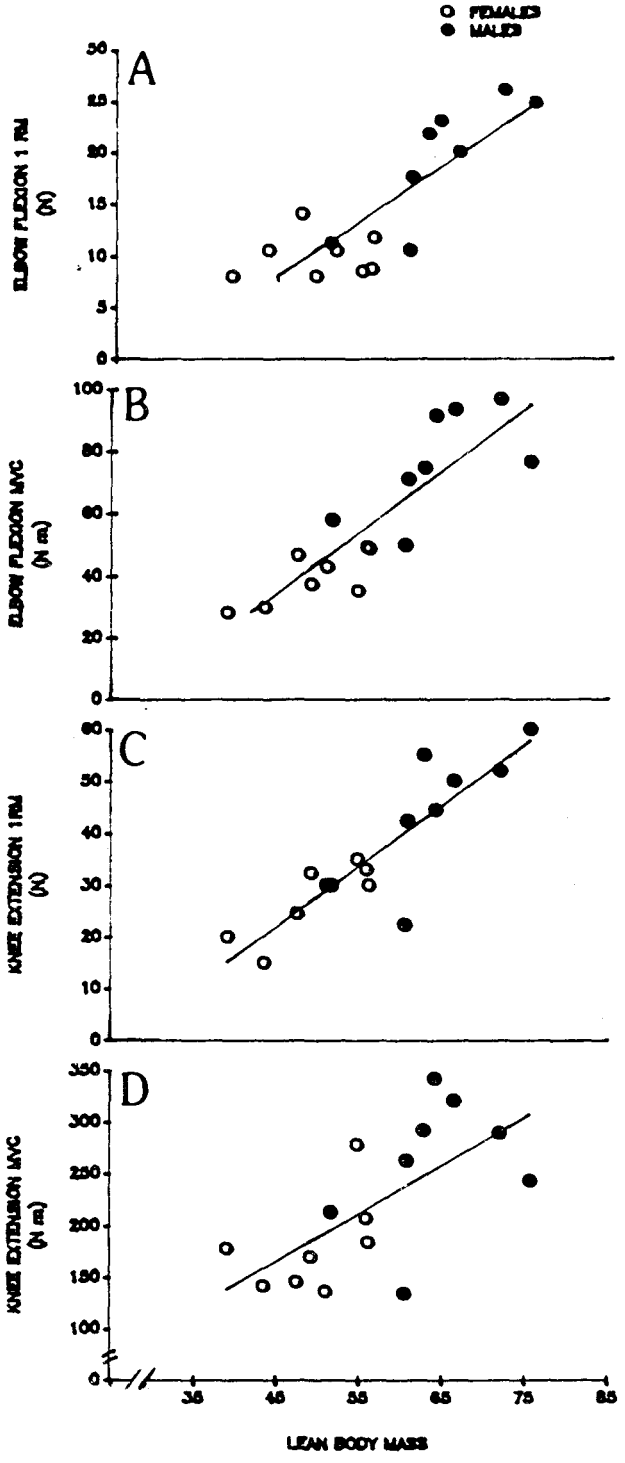

FEMALES
MALES
A
ELBOW FLEXION 1 RM (N)
B
ELBOW FLEXION MVC (N m)
C
KNEE EXTENSION 1RM (N)
D
KNEE EXTENSION MVC (N m)
LEAN BODY MASS

FIGURE 5: A. STRENGTH (TWITCH TORQUE) TO CROSS-SECTIONAL AREA RATIO OF THE ELBOW FLEXORS AND KNEE EXTENSORS

Elbow Flexors n = 7 for females, 8 for males
Knee Extensors n = 8 for females, 8 for males
Values are means $\pm$ SE

B. STRENGTH (MVC) TO CROSS-SECTIONAL AREA RATIO OF THE ELBOW FLEXORS AND KNEE EXTENSORS

Elbow Flexors n = 7 for females, 8 for males
Knee Extensors n = 8 for females, 8 for males
Values are means $\pm$ SE

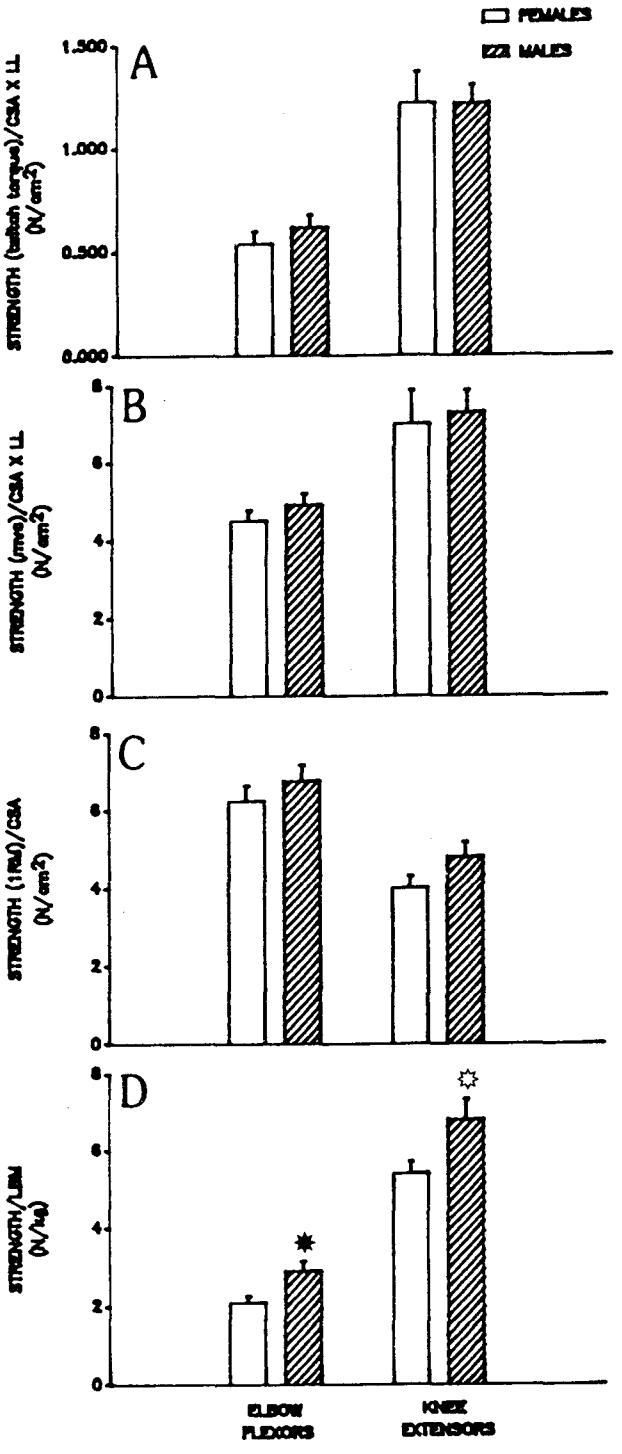
C. STRENGTH (1RM) TO CROSS-SECTIONAL AREA RATIO OF THE ELBOW FLEXORS AND KNEE EXTENSORS

Elbow Flexors n =7 for females, 8 for males
Knee Extensors n = 8 for females, 8 for males
Values are means $\pm$ SE

D. STRENGTH TO LEAN BODY MASS RATIO OF THE ELBOW FLEXORS AND KNEE EXTENSORS

n = 8 for females, 8 for males
Values are means $\pm$ SE
☼ $p \leq 0.05$, ✸ $p \leq 0.01$ for differences between female and male groups

Note: To correct for moment arm length in the twitch torque and MVC measurements (N m), muscle cross-sectional area (cm) was multiplied by the limb length (m) The strength to cross-sectional ratio is therefore expressed as N/cm .


FEMALES
MALES
A
B
C
D
1.500
1.000
0.500
0.000
STRENGTH (twitch torque)/CSA X LL
(N/cm²)
STRENGTH (mvc)/CSA X LL
(N/cm²)
STRENGTH (1RM)/CSA
(N/cm²)
STRENGTH/LBM
(N/kg)
ELBOW
FLEXORS
KNEE
EXTENSORS

2.3.4 Muscular Endurance

A. Elbow Flexion. Gender differences in muscular endurance for elbow flexion are illustrated in Figure 6. Females performed significantly more repetitions than the males at a load corresponding to 60% of the 1RM (38 ± 5 vs. 21 ± 3, $p \leq 0.01$)

B. Knee Extension. Gender differences in muscular endurance for knee extension are illustrated in Figure 7. No significant gender differences were found in the number of repetitions that could be performed at loads corresponding to 40 and 60% of the 1RM.

2.3.5 Muscle Cross-Sectional Area

A significant postitive correlation was found between the knee extensors 1RM and knee extensors CSA ($r=.84$, $p \leq 0.01$) (Figure 8). A significant positive correlation was also found between the elbow flexors 1RM and elbow flexors CSA ($r=.95$, $p \leq 0.01$) (Figure 9). Strength, measured as torque, is a function of muscular force and muscle moment arm length. Although not measured directly, the muscle moment arm length was considered proportional to limb length. A significant positive correlation was found between the knee extensors MVC and the product of knee extensor CSA and upper leg length ($r=.61$, $p \leq 0.05$) (Figure 10). The elbow flexors MVC was

FIGURE 6: MUSCULAR ENDURANCE OF THE ELBOW FLEXORS AT 60% OF THE 1 RM

n = 7 for females, 8 for males
Values are means $\pm$ SE
* $p \leq 0.01$ for differences between female and male groups

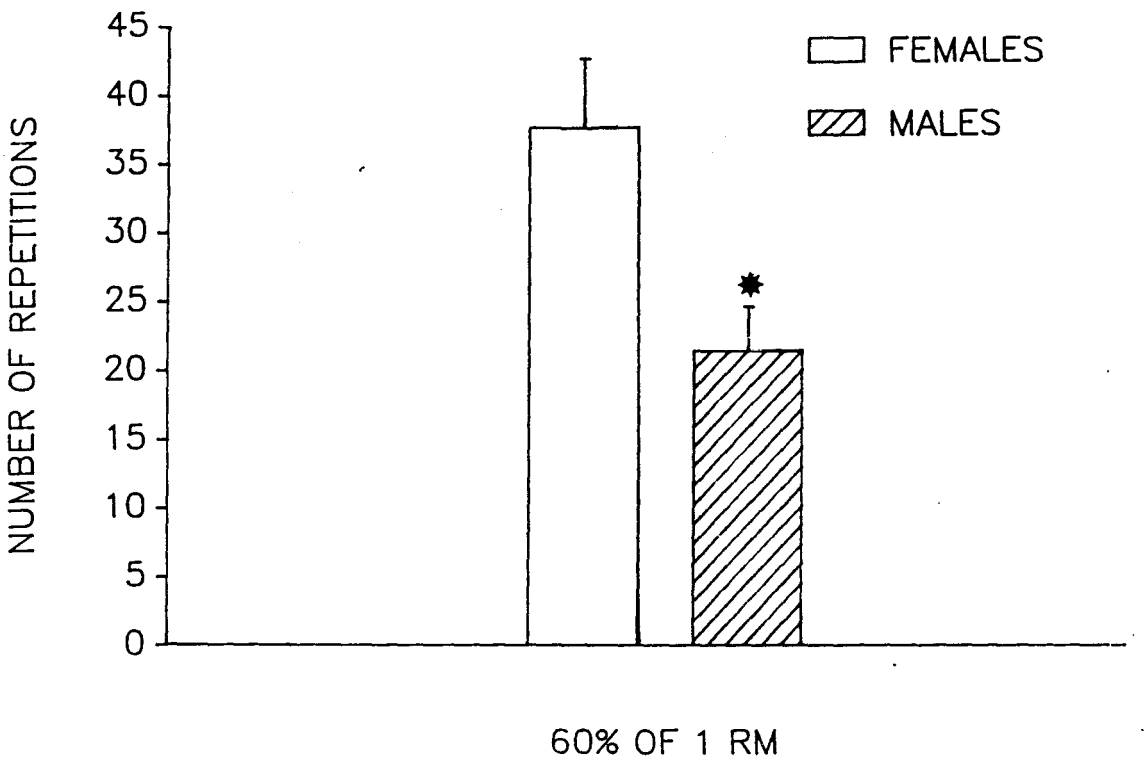

45
40
35
30
25
20
15
10
5
0
NUMBER OF REPETITIONS
FEMALES
MALES
60% OF 1 RM

FIGURE 7: MUSCULAR ENDURANCE OF THE KNEE EXTENSORS AT 40 AND 60% OF THE 1RM

40% condition n = 7 for females, 8 for males
60% condition n = 8 for females, 8 for males
Values are means $\pm$ SE

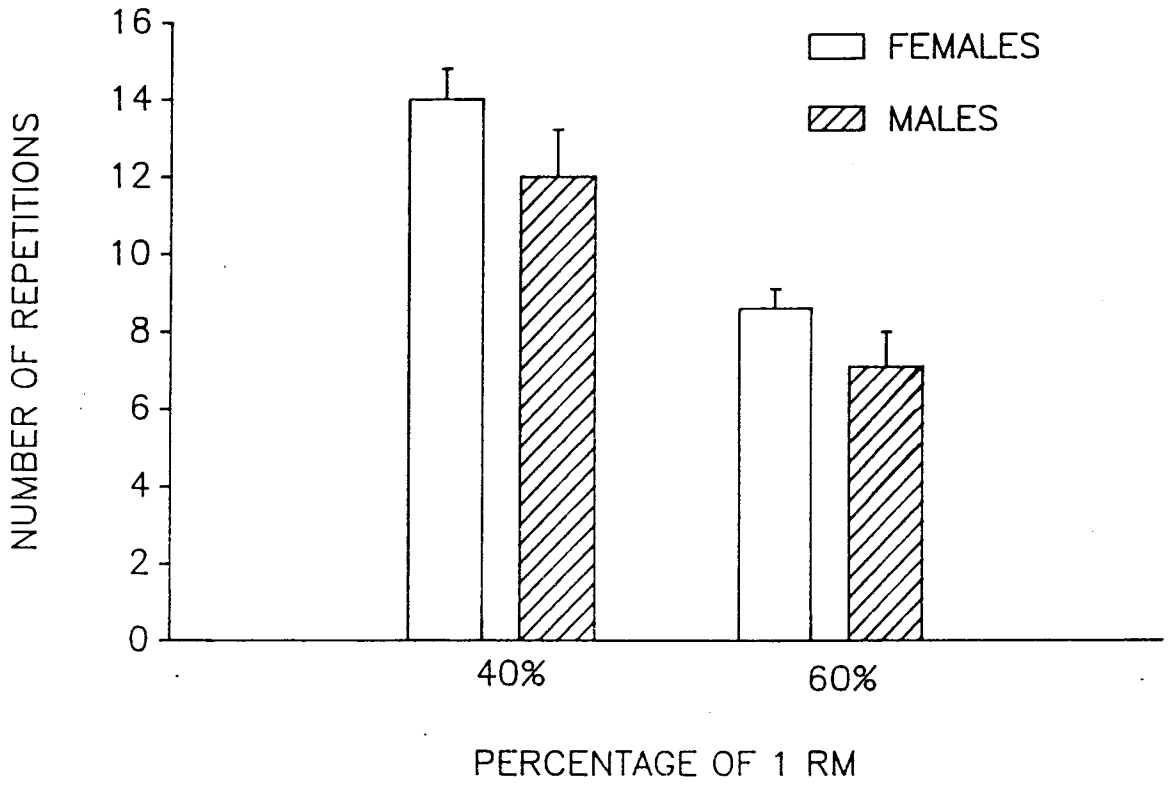

16
14
12
10
8
6
4
2
0
NUMBER OF REPETITIONS
FEMALES
MALES
40%
60%
PERCENTAGE OF 1 RM

FIGURE 8: CORRELATION OF STRENGTH (1RM) AND KNEE EXTENSOR CROSS-SECTIONAL AREA

n = 8 for females, 8 for males
r = .84 ($p \leq 0.01$)
y = .72 (x) + 20.33

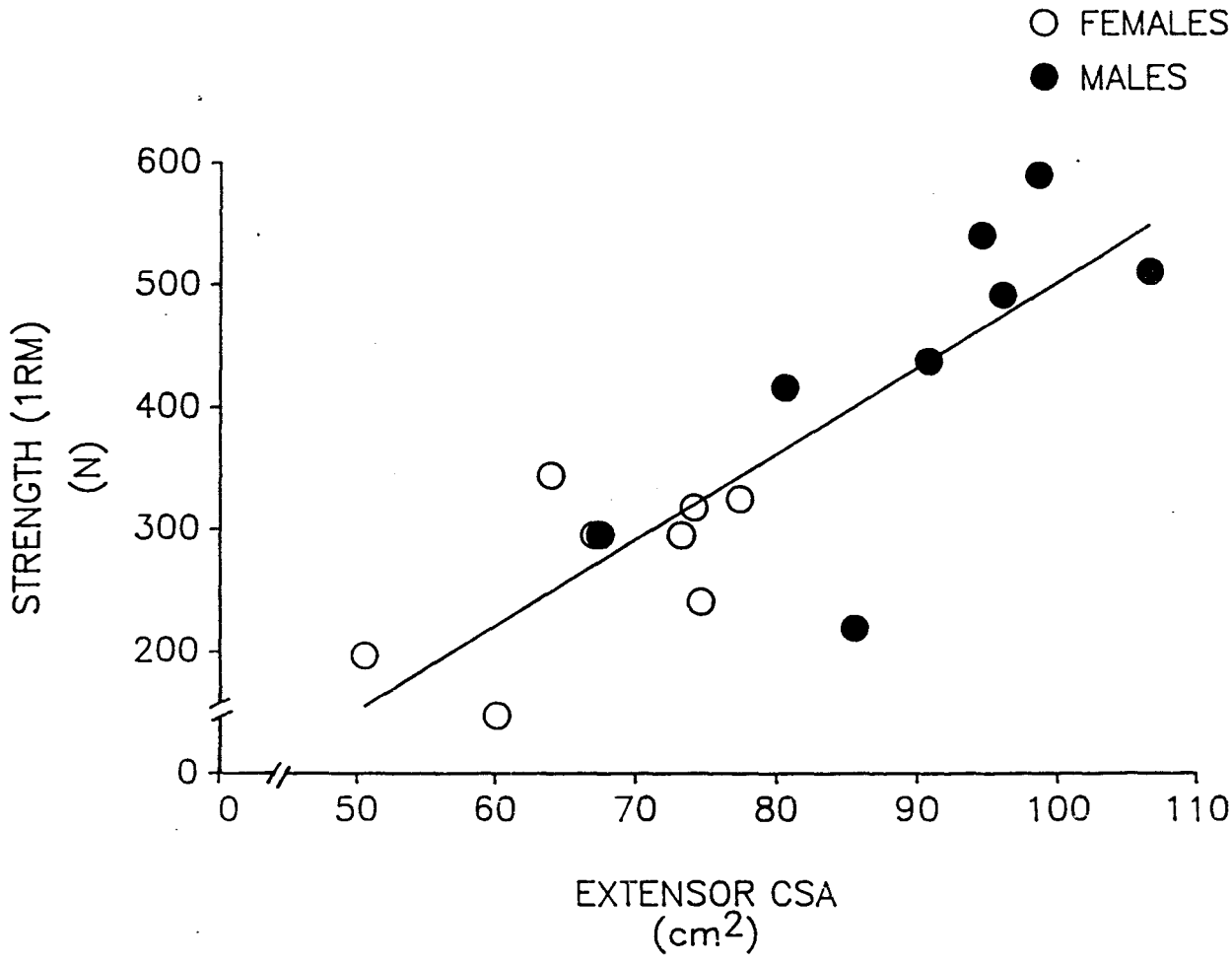

FEMALES
MALES
STRENGTH (1RM)
(N)
600
500
400
300
200
0
0
50
60
70
80
90
100
110
EXTENSOR CSA
(cm2)

FIGURE 9: CORRELATION OF STRENGTH (1RM) AND ELBOW FLEXOR CROSS-SECTIONAL AREA

$n = 7$ for females, 8 for males
$r = .95$ ($p \leq 0.01$)
$y = .85(x) - 3.8$

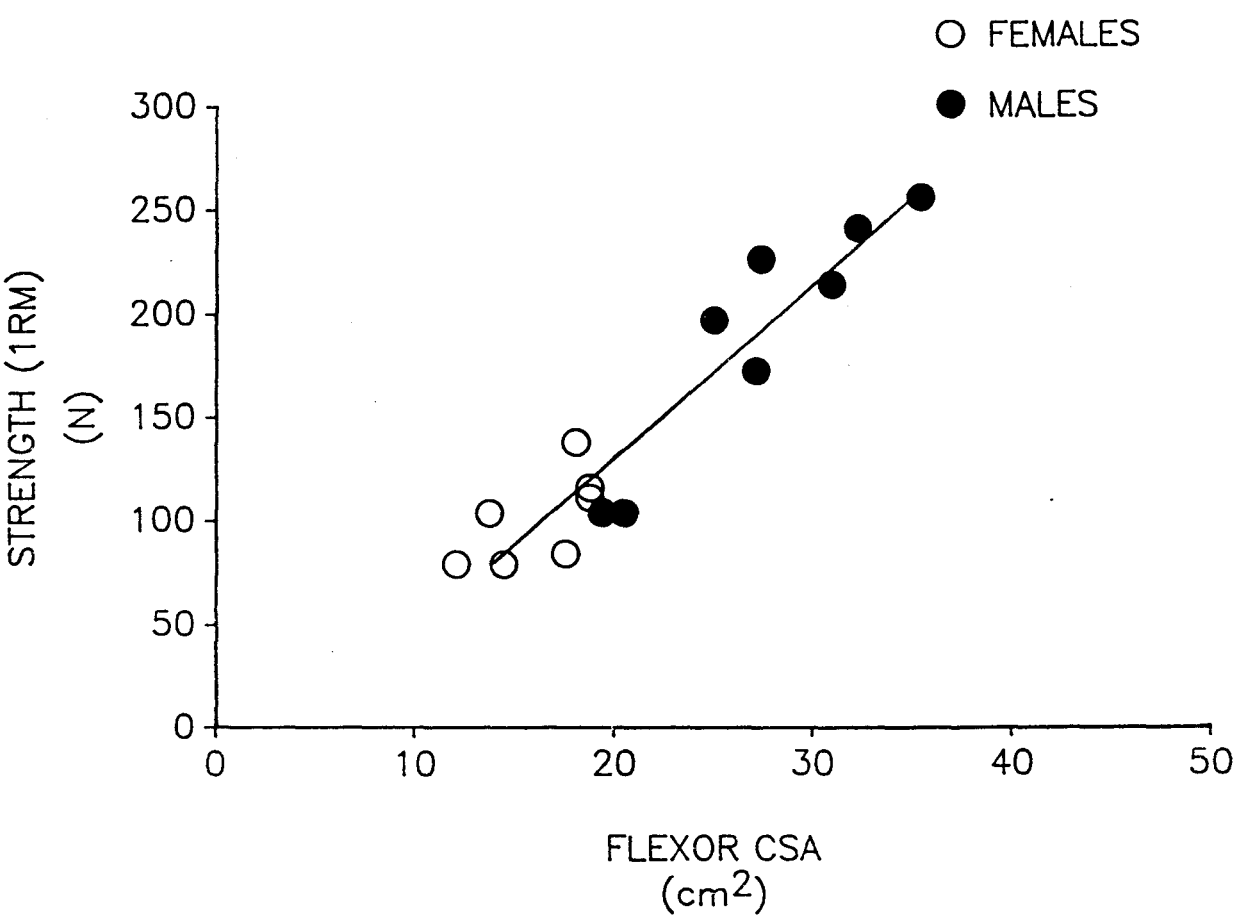
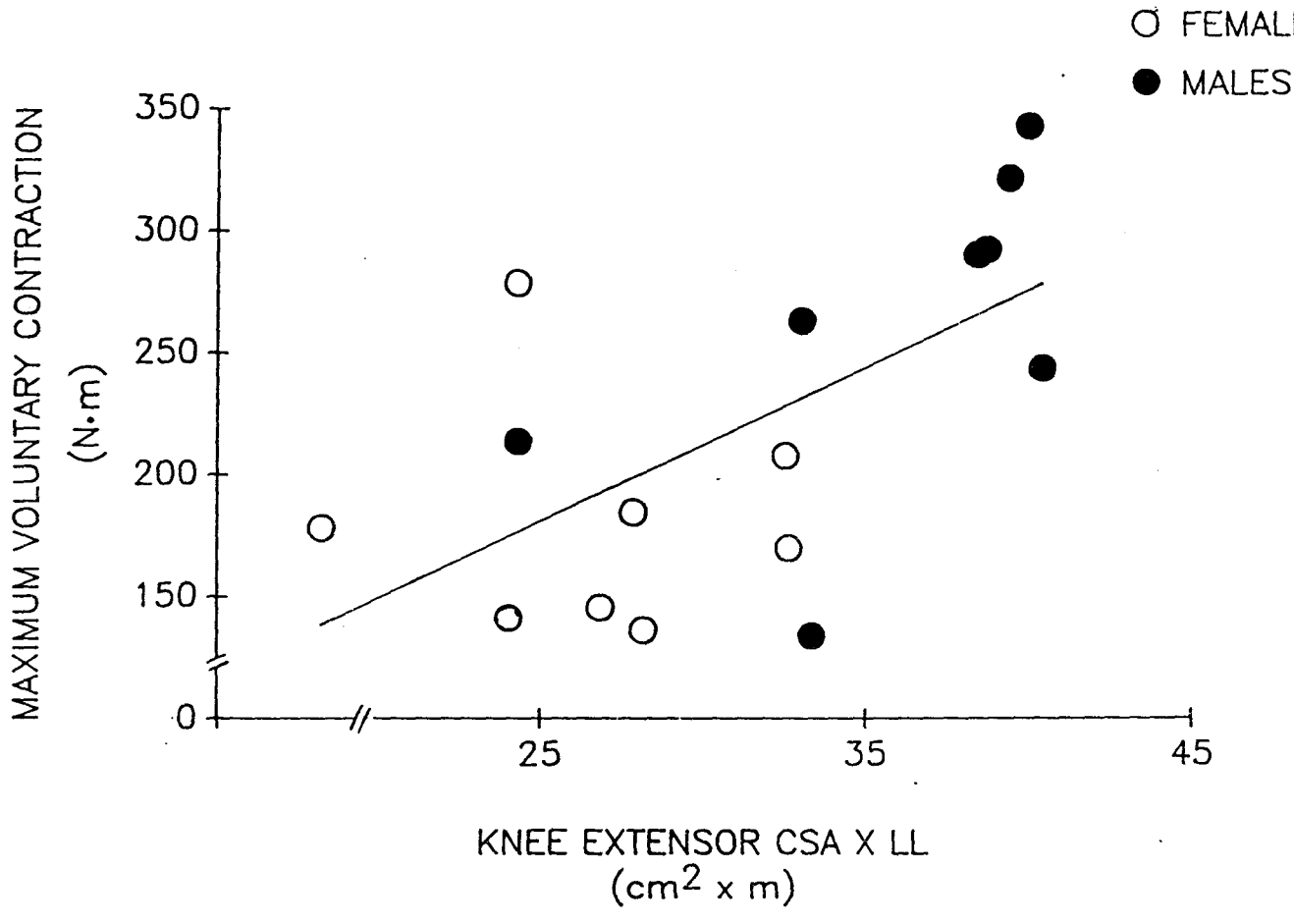

FEMALES
MALES
300
250
200
150
100
50
0
STRENGTH (1RM)
(N)
0
10
20
30
40
50
FLEXOR CSA
(cm2)

FIGURE 10: CORRELATION OF KNEE EXTENSOR STRENGTH (MVC) AND THE PRODUCT OF KNEE EXTENSOR CROSS-SECTIONAL AREA AND FEMUR LENGTH

$n = 8$ for females, 8 for males
$r = .61$ ($p \leq 0.05$)
$y = 6.2(x) + 27.8$


FEMALES
MALES
MAXIMUM VOLUNTARY CONTRACTION
(N·m)
350
300
250
200
150
0
25
35
45
KNEE EXTENSOR CSA X LL
(cm2 x m)

positively correlated with the product of elbow flexor CSA and arm length ($r=.91$, $p \leq 0.01$) (Figure 11).

Gender differences in muscle CSA are illustrated in Figure 12. The cross-sectional areas of the females were 45%, 41%, 30%, and 25% smaller than the males for the biceps brachii, elbow flexors, vastus lateralis and knee extensors respectively ($p \leq 0.01$) Females had significantly higher proportions of collagen and other non-contractile tissue in the vastus lateralis (18.6% $\pm$ 1.6 vs. 14.8% $\pm$ .7, $p \leq 0.05$) than males (Figure 13). No significant difference was found in the proportion of collagen and other non-contractile tissue in the biceps brachii between males (14.2% $\pm$ 1.5) and females (17.7% $\pm$ .9). Differences in muscle CSA were significant whether or not muscle area was corrected for collagen (Figure 12).

2.3.6 Ratio of Strength to Muscle CSA

The strength to CSA ratios are presented in Figure 5. No significant gender difference was found to exist in the strength to CSA ratios for either the elbow flexors or the knee extensors regardless of whether strength was expressed as the 1RM (newtons) (Figure 5C), the MVC (newton metres) (Figure 5B), or twitch torque (newton metres) (Figure 5A).

FIGURE 11: CORRELATION OF ELBOW FLEXOR STRENGTH (MVC) AND THE PRODUCT OF ELBOW FLEXOR CROSS-SECTIONAL AREA AND TOTAL ARM LENGTH

$n = 7$ for females, 8 for males
$r = .91$ ($p \leq 0.01$)
$y = 4.8(x) - .94$

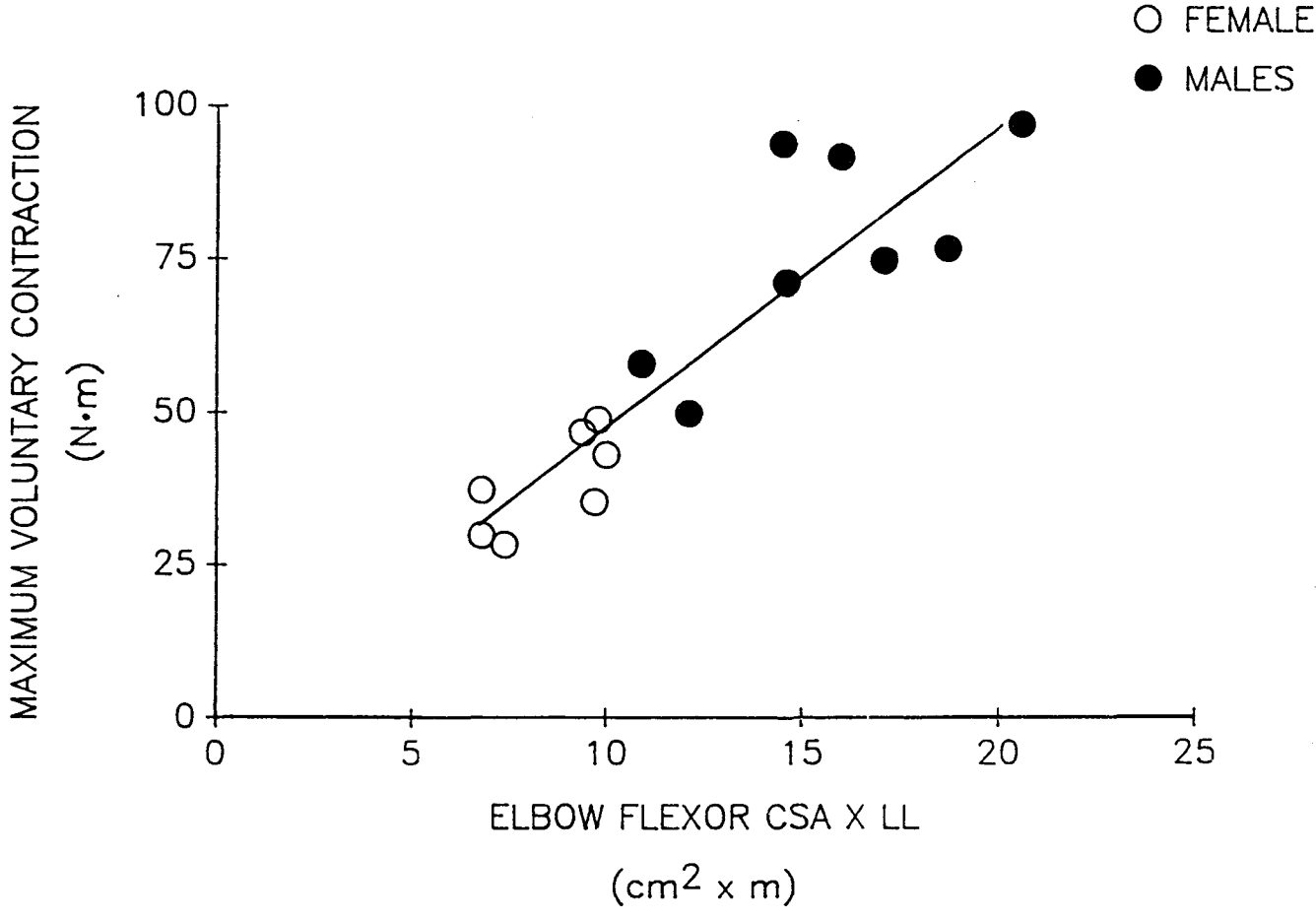

FEMALE
MALES
MAXIMUM VOLUNTARY CONTRACTION
(N·m)
100
75
50
25
0
0
5
10
15
20
25
ELBOW FLEXOR CSA X LL
(cm2 x m)

FIGURE 12: A. VASTUS LATERALIS CROSS-SECTIONAL AREA

n = 8 for females, 8 for males
Values are means ± SE
✱p ≤ 0.01 for differences between female and male groups

B. KNEE EXTENSOR CROSS-SECTIONAL AREA

n = 8 for females, 8 for males
Values are means ± SE
✱p ≤ 0.01 for differences between female and male groups

C. BICEPS BRACHII CROSS-SECTIONAL AREA

n = 7 for females, 8 for males
Values are means ± SE
✱p ≤ 0.01 for differences between female and male groups

D. ELBOW FLEXOR CROSS-SECTIONAL AREA

n = 7 for females, 8 for males
Values are means ± SE
✱p ≤ 0.01 for differences between female and male groups

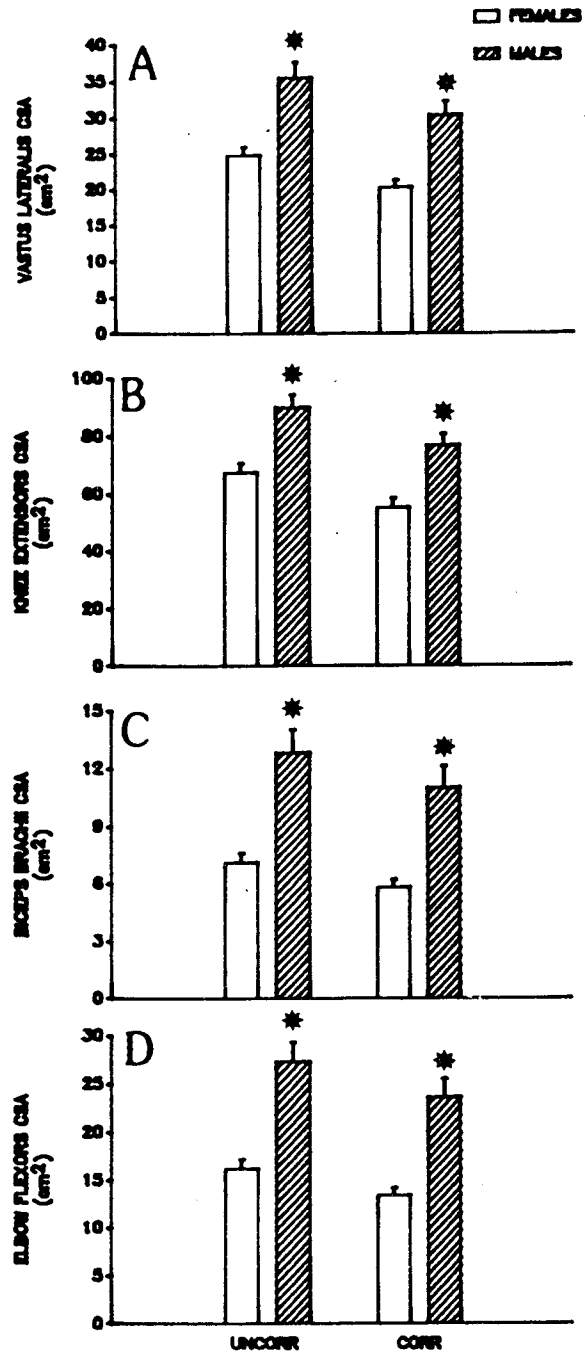
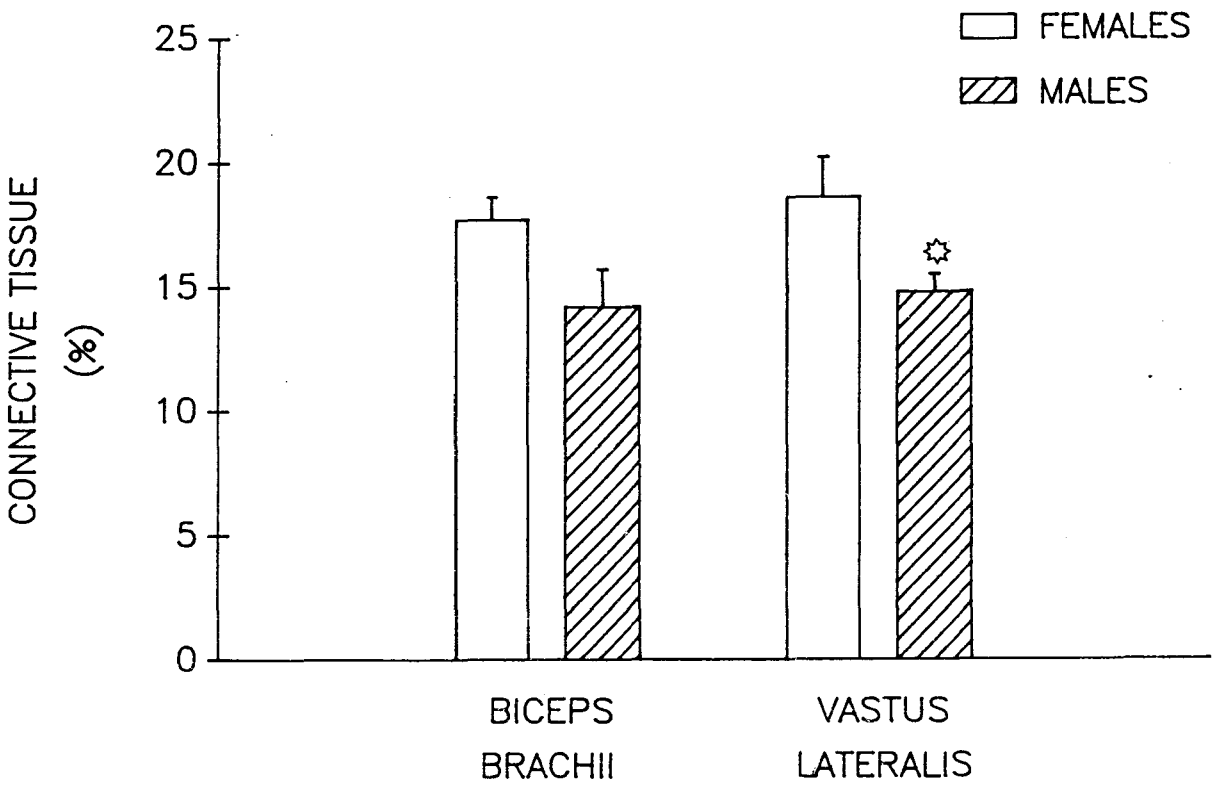

FEMALES
MALES
A
B
C
D
VASTUS LATERALIS CSA (cm²)
KNEE EXTENSORS CSA (cm²)
BICEPS BRACHII CSA (cm²)
ELBOW FLEXORS CSA (cm²)
UNCORR
CORR

FIGURE 13: PERCENTAGE OF CONNECTIVE TISSUE IN THE BICEPS BRACHII AND VASTUS LATERALIS

Biceps Brachii n = 6 for females, 7 for males
Vastus Lateralis n = 7 for females, 7 for males
Values are means $\pm$ SE
$\Diamond p \leq 0.05$ for differences between female and male groups


FEMALES
MALES
CONNECTIVE TISSUE (%)
25
20
15
10
5
0
BICEPS BRACHII
VASTUS LATERALIS

2.3.7 Muscle Fiber Characteristics

A. Biceps Brachii. Muscle fiber area according to fiber type in the biceps is illustrated in Figure 14. In females, the type II fibers ($4306\ um^2 \pm 556$) were significantly larger than the type I fibers ($3483\ um^2 \pm 339$) ($p \leq 0.05$). A large difference in type I ($4597\ um^2 \pm 396$) and type II ($8207\ um^2 \pm 1832$) fiber area was found in males; however, this difference did not achieve statistical significance. Males had significantly larger type I fibers than females ($p \leq 0.05$) (Figure 14C). The difference in type II fiber size was not statistically significant despite the fact the these fibers were almost twice as large in the males as in the females (Figure 14D). The mean fiber area in males ($6632\ um^2 \pm 1160$) was significantly larger than that in the females ($3963\ um^2 \pm 450$) ($p \leq 0.05$) (Figure 15B).

No significant difference was found in fiber type distribution in male ($57.0\% \pm 1.7$ type II) and female biceps ($56.5\% \pm 3.3$ type II) (Figure 14A). The percentage of total muscle CSA occupied by type II fibers did not differ significantly between the sexes (Figure 14B).

No significant difference was found between males (180,620) and females (156,872) in biceps fiber number (Figure 15B).

FIGURE 14: A. PERCENT TYPE II FIBERS IN THE BICEPS BRACHII AND VASTUS LATERALIS

n = 7 for females, 7 for males
Values are means ± SE
✸p ≤ 0.01 for differences between female and male groups

B. PERCENT TYPE II FIBER AREA IN THE BICEPS BRACHII AND VASTUS LATERALIS

n = 7 for females, 7 for males
Values are means ± SE
✸p ≤ 0.01 for differences between female and male groups

C. TYPE I FIBER AREA IN BICEPS BRACHII AND VASTUS LATERALIS

Biceps Brachii n = 7 for females, 7 for males
Vastus Lateralis n = 5 for females, 8 for males Values are means ± SE
☼p ≤ 0.05 for differences between female and male groups

D. TYPE II FIBER AREA IN BICEPS BRACHII AND VASTUS LATERALIS

Biceps Brachii n = 7 for females, 7 for males
Vastus Lateralis n = 5 for females, 8 for males Values are means ± SE
✸p ≤ 0.01 for differences between female and male groups, †p ≤ 0.05 for differences in type I and type II fiber size within gender groups

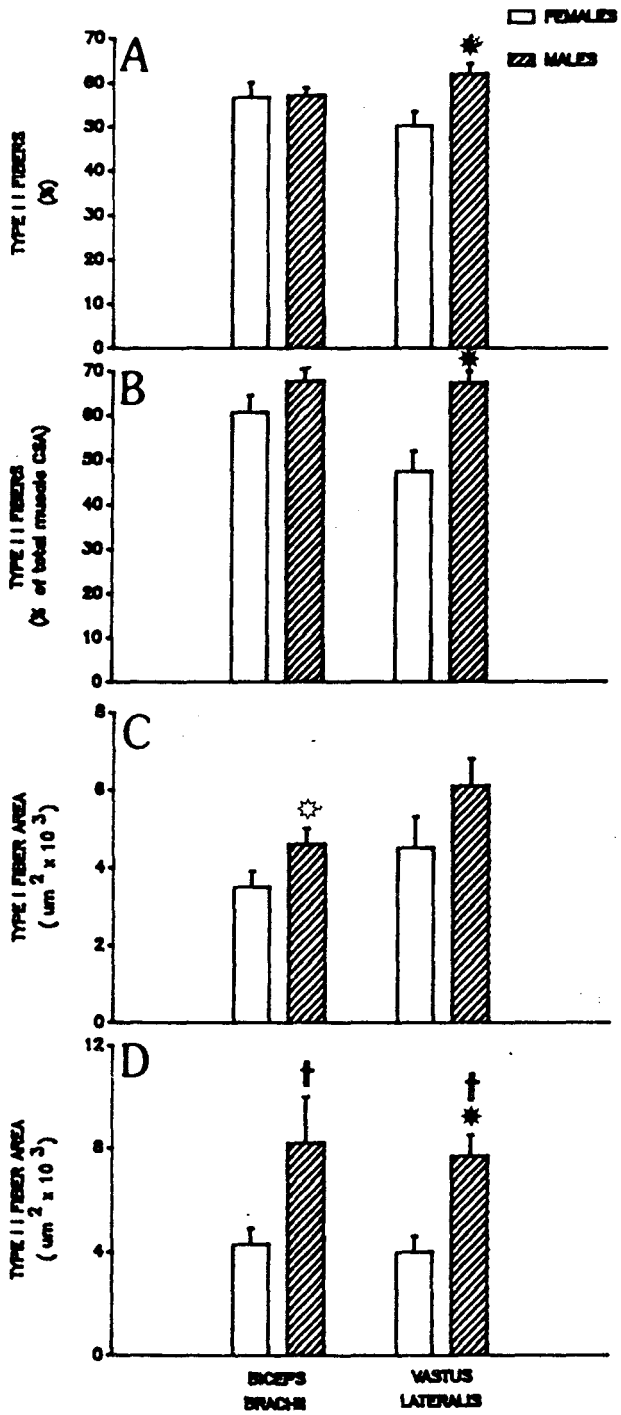
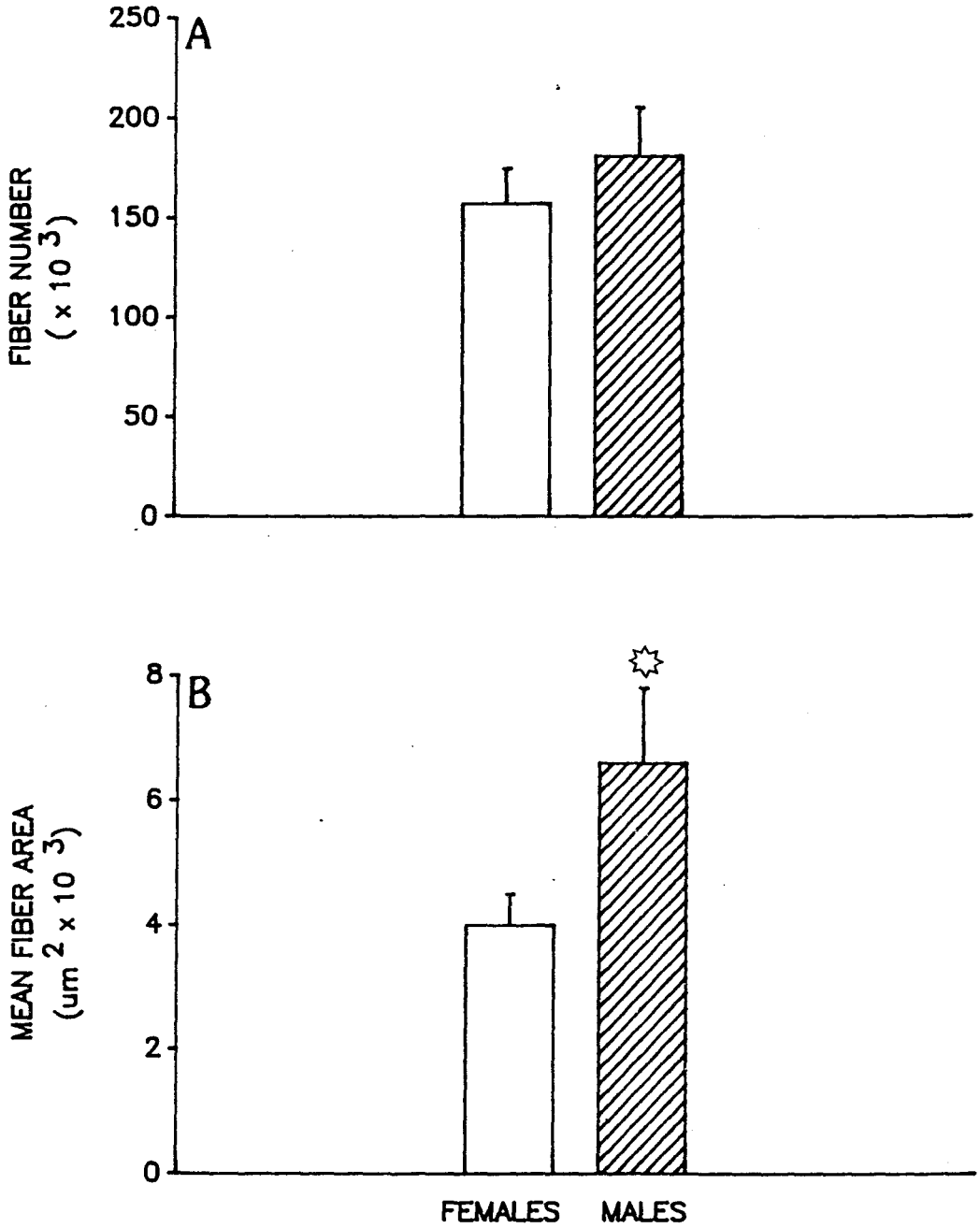

FEMALES
MALES
A
B
C
D
TYPE I I FIBERS (%)
TYPE I I FIBERS (% of total muscle CSA)
TYPE I FIBER AREA (um 2 x 10 3)
TYPE I I FIBER AREA (um 2 x 10 3)
BICEPS BRACHII
VASTUS LATERALIS

FIGURE 15: A. FIBER NUMBER IN BICEPS BRACHII

n = 7 for females, 8 for males
Values are means ± SE

B. MEAN FIBER AREA IN BICEPS BRACHII

n = 7 for females, 7 for males
Values are means ± SE
✡ $p \leq 0.05$ for differences between female and male groups


A
250
200
150
100
50
0
FIBER NUMBER
(x 10 3)
B
8
6
4
2
0
MEAN FIBER AREA
(um 2 x 10 3)
FEMALES
MALES

A significant positive correlation was found between biceps mean fiber area and biceps CSA ($r=.56$, $p \leq 0.05$) (Figure 16A). No significant correlation was found between biceps fiber number and biceps CSA (Figure 16B).

B. Vastus Lateralis. Muscle fiber area according to fiber type in the vastus lateralis is illustrated in Figure 14. The type II fibers ($7700\ um^2 \pm 799$) were significantly larger than the type I fibers ($6142\ um^2 \pm 747$) in the males ($p \leq 0.05$). No significant difference between type I ($4531\ um^2$ 806) and type II ($4040\ um^2 \pm 618$) fiber size was found in the females. Males had significantly larger type II fibers than the females ($p \leq 0.01$) (Figure 14D). No significant gender difference in the size of the type I fibers was found (Figure 14C). The mean fiber area in males ($7070\ um^2 \pm 699$) was significantly larger than that in the females ($4290\ um^2 \pm 655$) ($p \leq 0.05$) (Figure 17B).

A significant difference in fiber type compostition of the vastus lateralis was found between the males ($61.9\% \pm 2.2$ type II) and females ($50.2\% \pm 3.1$ type II) ($p \leq 0.01$) (Figure 14A). The percentage of total muscle CSA occupied by type II fibers was significantly greater in the males ($67.4\% \pm 2.6$) than the females ($47.4\% \pm 4.4$)($p \leq 0.01$) (Figure 14B).

No significant difference was found between males (451,468) and females (465,007) in the muscle area to fiber area ratio (Figure 17A).

FIGURE 16: A. CORRELATION OF MEAN FIBER AREA AND CROSS-SECTIONAL AREA OF THE BICEPS BRACHII

n = 7 for females, 8 for males
$r = .56$ ($p \leq 0.05$)
$y = 414.4(x) + 1883.4$

B. CORRELATION OF FIBER NUMBER AND CROSS-SECTIONAL AREA OF THE BICEPS BRACHII

n = 7 for females, 8 for males

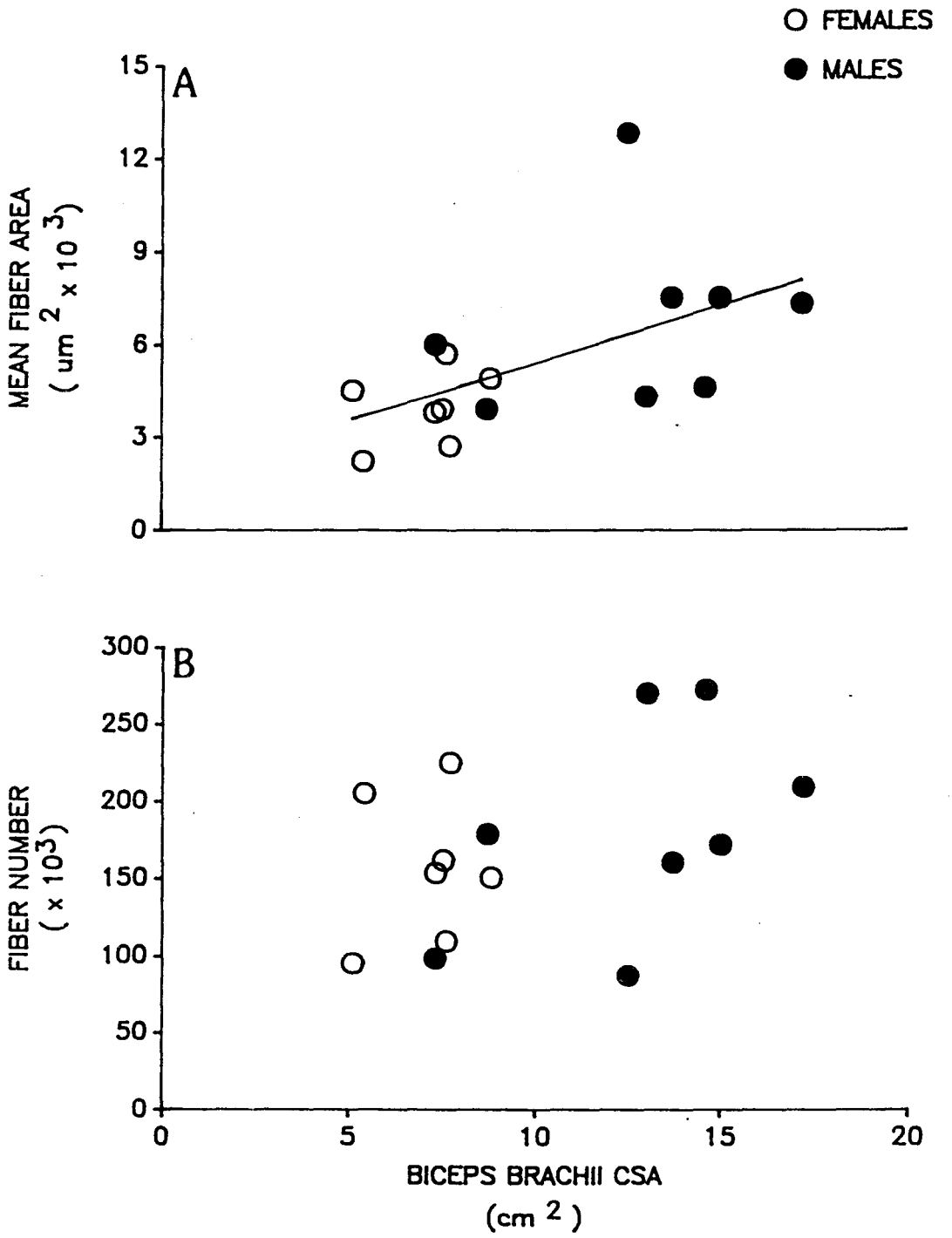
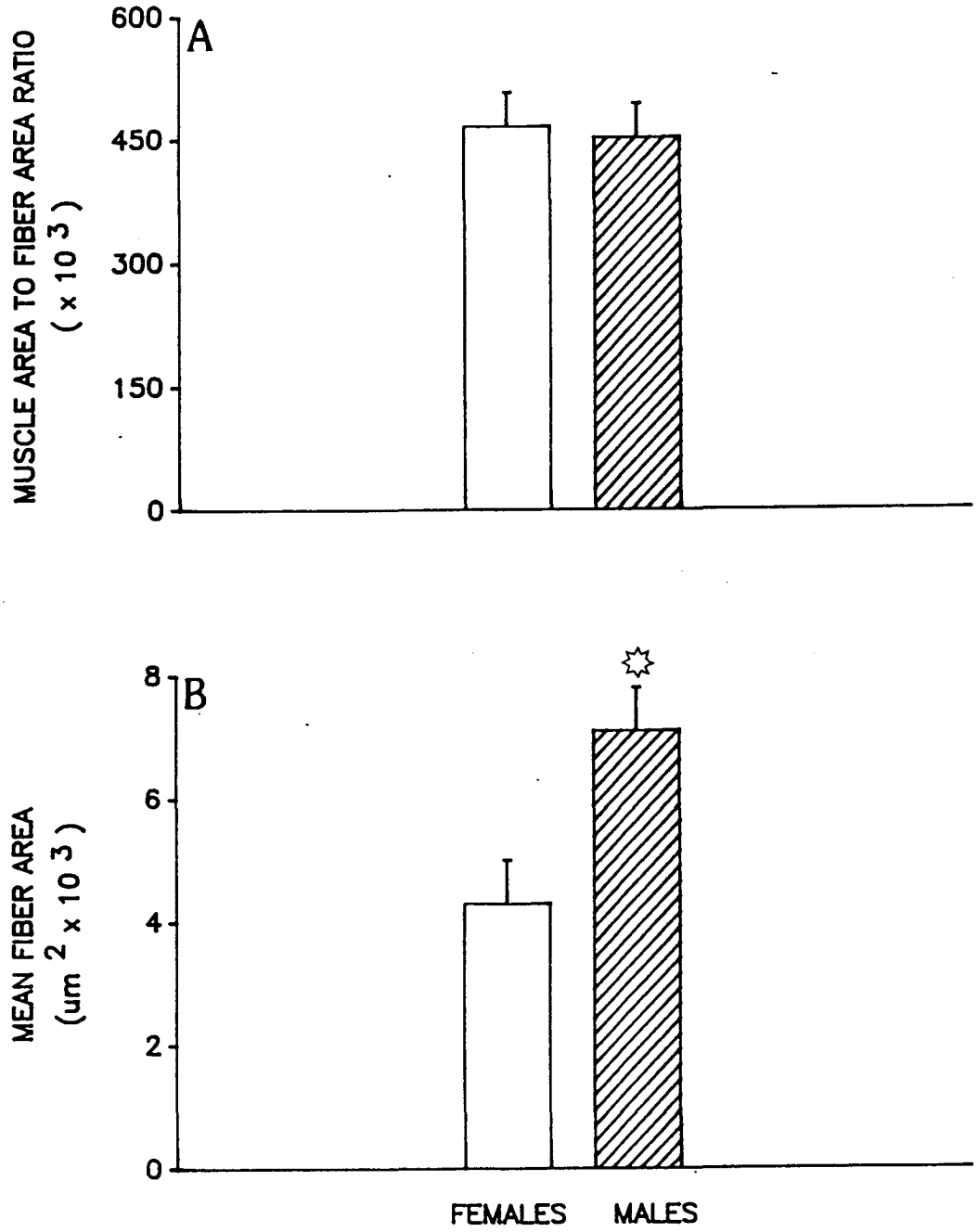

O FEMALES
● MALES
A
MEAN FIBER AREA
(um 2 x 10 3)
15
12
9
6
3
0
B
FIBER NUMBER
(x 10 3)
300
250
200
150
100
50
0
0
5
10
15
20
BICEPS BRACHII CSA
(cm 2)

FIGURE 17: A. MUSCLE AREA TO FIBER AREA RATIO IN THE VASTUS LATERALIS

n = 8 for females, 8 for males
Values are means ± SE

B. MEAN FIBER AREA IN VASTUS LATERALIS

n = 5 for females, 8 for males
Values are means ± SE
☼ $p \leq 0.05$ for differences between female and male groups


A
600
450
300
150
0
MUSCLE AREA TO FIBER AREA RATIO
(x 10 3)
B
8
6
4
2
0
MEAN FIBER AREA
(um 2 x 10 3)
FEMALES
MALES

A significant positive correlation was found between vastus lateralis mean fiber area and vastus lateralis CSA ($r=.69$, $p \leq 0.01$) (Figure 18A). No significant correlation was found between the muscle area to fiber area ratio and vastus lateralis CSA (Figure 18B).

2.3.8 Percent Type II Fiber Area and Strength/CSA Ratios

A. Elbow Flexion. The percent type II fiber area of the biceps brachii failed to correlate with any of the strength/CSA ratios of the elbow flexors (Figures 19A, 19B and 19C).

B. Knee Extension. The percent type II fiber area of the vastus lateralis failed to correlate with the strength/CSA ratio when knee extensor strength was expressed as an MVC (Figure 20B) or twitch torque (Figure 20A). A significant postitive correlation was found between the percent type II fiber area of the vastus lateralis and the knee extensor strength/CSA ratio when strength was expressed as a 1RM ($r=.75$, $p \leq 0.01$) (Figure 20C). This correlation, however, was not found within each gender group.

2.3.9 Motor Unit Characteristics

Motor unit characteristics for the biceps brachii and vastus medialis are presented in Figures 21, 22 and 23. No significant difference in motor unit number for either the biceps brachii or the

FIGURE 18: A. CORRELATION OF MEAN FIBER AREA AND CROSS-SECTIONAL AREA OF THE VASTUS LATERALIS

n = 8 for females, 8 for males
$r = .69$ ($p \leq 0.01$)
$y = 214.1(x) + 416.6$

B. CORRELATION OF MUSCLE AREA TO FIBER AREA RATIO AND CROSS-SECTIONAL AREA OF THE VASTUS LATERALIS

n = 8 for females, 8 for males

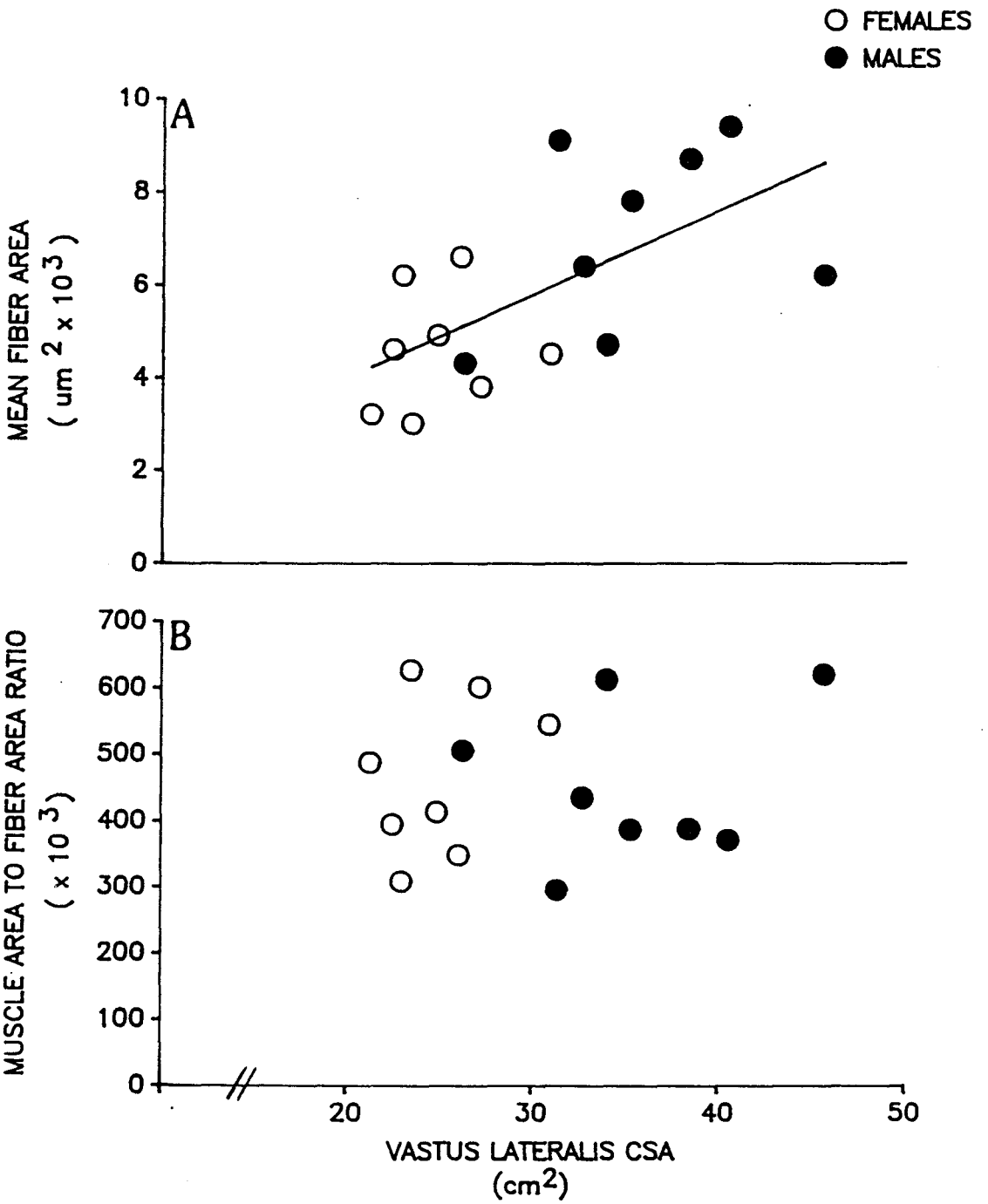

FEMALES
MALES
A
MEAN FIBER AREA
(um 2 x 10 3)
10
8
6
4
2
0
B
MUSCLE AREA TO FIBER AREA RATIO
(x 10 3)
700
600
500
400
300
200
100
0
20
30
40
50
VASTUS LATERALIS CSA
(cm2)

FIGURE 19: A. CORRELATION OF ELBOW FLEXOR STRENGTH (TWITCH TORQUE) TO CROSS-SECTIONAL AREA RATIO AND PERCENT TYPE II FIBER AREA IN THE BICEPS BRACHII

n = 7 for females, 7 for males

B. CORRELATION OF ELBOW FLEXOR STRENGTH (MVC) TO CROSS-SECTIONAL AREA RATIO AND PERCENT TYPE II FIBER AREA IN THE BICEPS BRACHII

n = 7 for females, 7 for males

C. CORRELATION OF ELBOW FLEXOR STRENGTH (1RM) TO CROSS-SECTIONAL AREA RATIO AND PERCENT TYPE II FIBER AREA IN THE BICEPS BRACHII

n = 7 for females, 7 for males

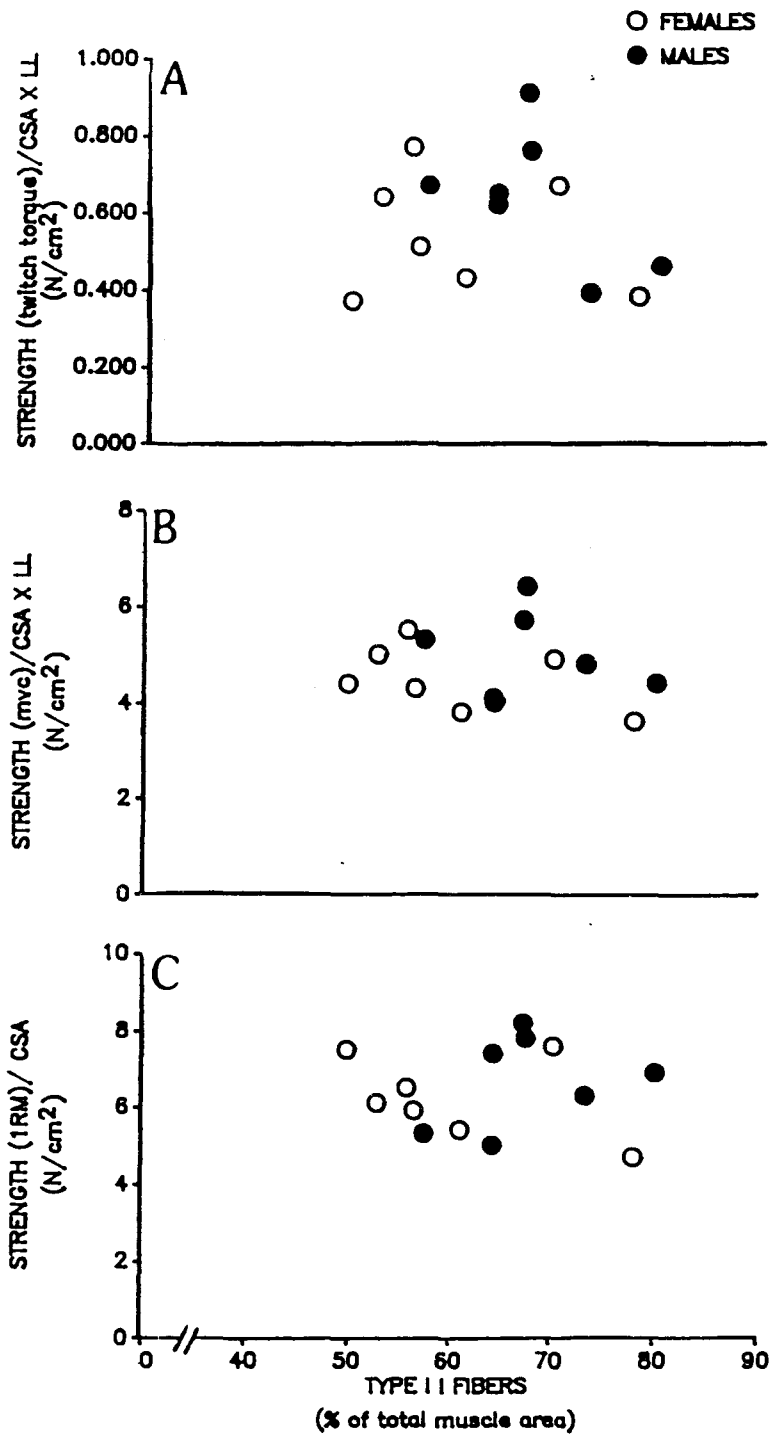

FEMALES
MALES
A
STRENGTH (twitch torque)/CSA X LL (N/cm²)
1.000
0.800
0.600
0.400
0.200
0.000
B
STRENGTH (mvc)/CSA X LL (N/cm²)
8
6
4
2
0
C
STRENGTH (1RM)/ CSA (N/cm²)
10
8
6
4
2
0
0
40
50
60
70
80
90
TYPE I I FIBERS
(% of total muscle area)

FIGURE 20: A. CORRELATION OF KNEE EXTENSOR STRENGTH (TWITCH TORQUE) TO CROSS-SECTIONAL AREA RATIO AND PERCENT TYPE II FIBER AREA IN THE VASTUS LATERALIS

n = 5 for females, 7 for males

B. CORRELATION OF KNEE EXTENSOR STRENGTH (MVC) TO CROSS-SECTIONAL AREA RATIO AND PERCENT TYPE II FIBER AREA IN THE VASTUS LATERALIS

n = 5 for females, 7 for males

C. CORRELATION OF KNEE EXTENSOR STRENGTH (1RM) TO CROSS-SECTIONAL AREA RATIO AND PERCENT TYPE II FIBER AREA IN THE VASTUS LATERALIS

n = 5 for females, 7 for males
$r = .75$ ($p \leq 0.01$)
$y = .06(x) + 1.02$

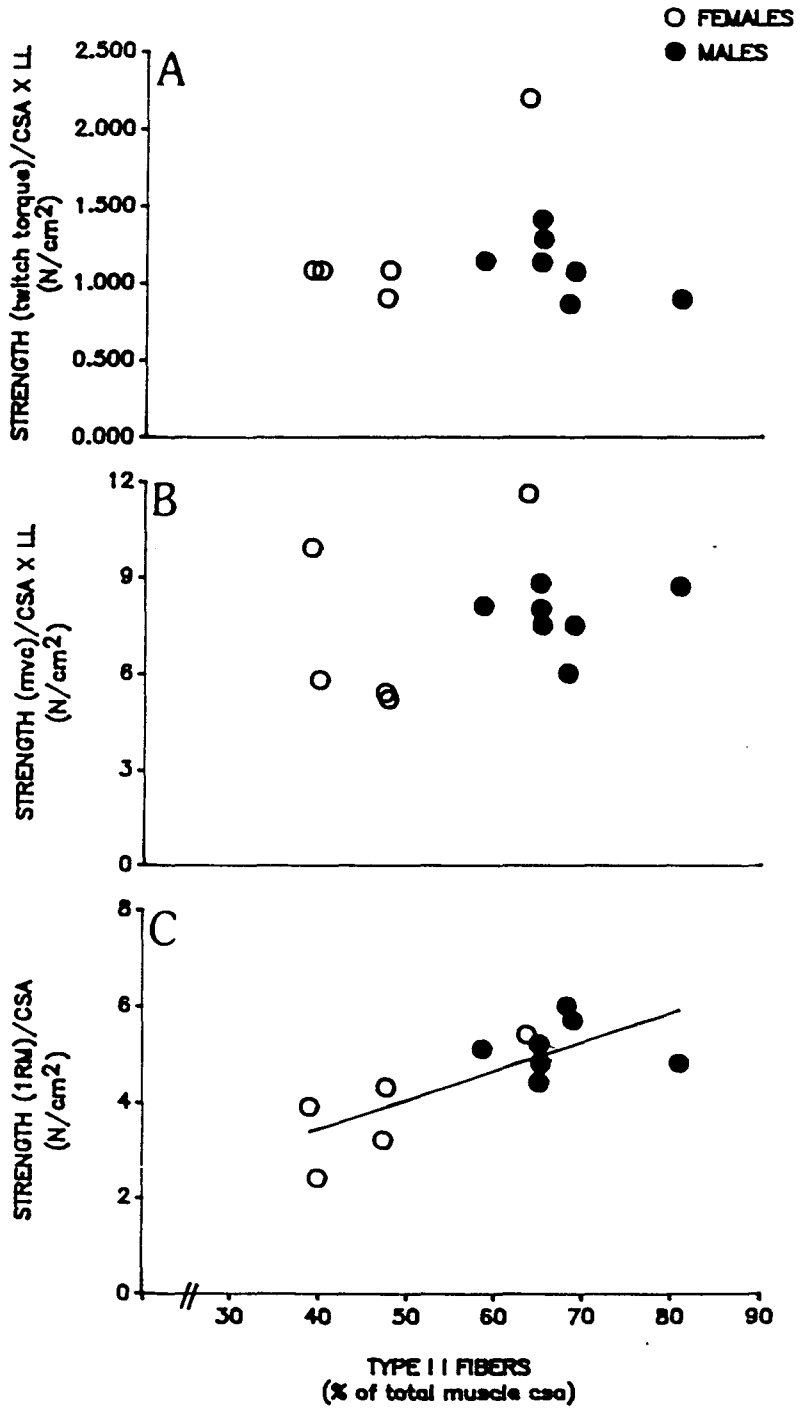

O FEMALES
● MALES
A
STRENGTH (twitch torque)/CSA X LL (N/cm²)
2.500
2.000
1.500
1.000
0.500
0.000
B
STRENGTH (mvc)/CSA X LL (N/cm²)
12
9
6
3
0
C
STRENGTH (1RM)/CSA (N/cm²)
8
6
4
2
0
30
40
50
60
70
80
90
TYPE I I FIBERS
(% of total muscle csa)

FIGURE 21: MOTOR UNIT NUMBER IN THE BICEPS BRACHII AND VASTUS MEDIALIS

Biceps Brachii n = 5 for females, 6 for males
Vastus Medialis n = 4 for females, 6 for males
Values are means $\pm$ SE

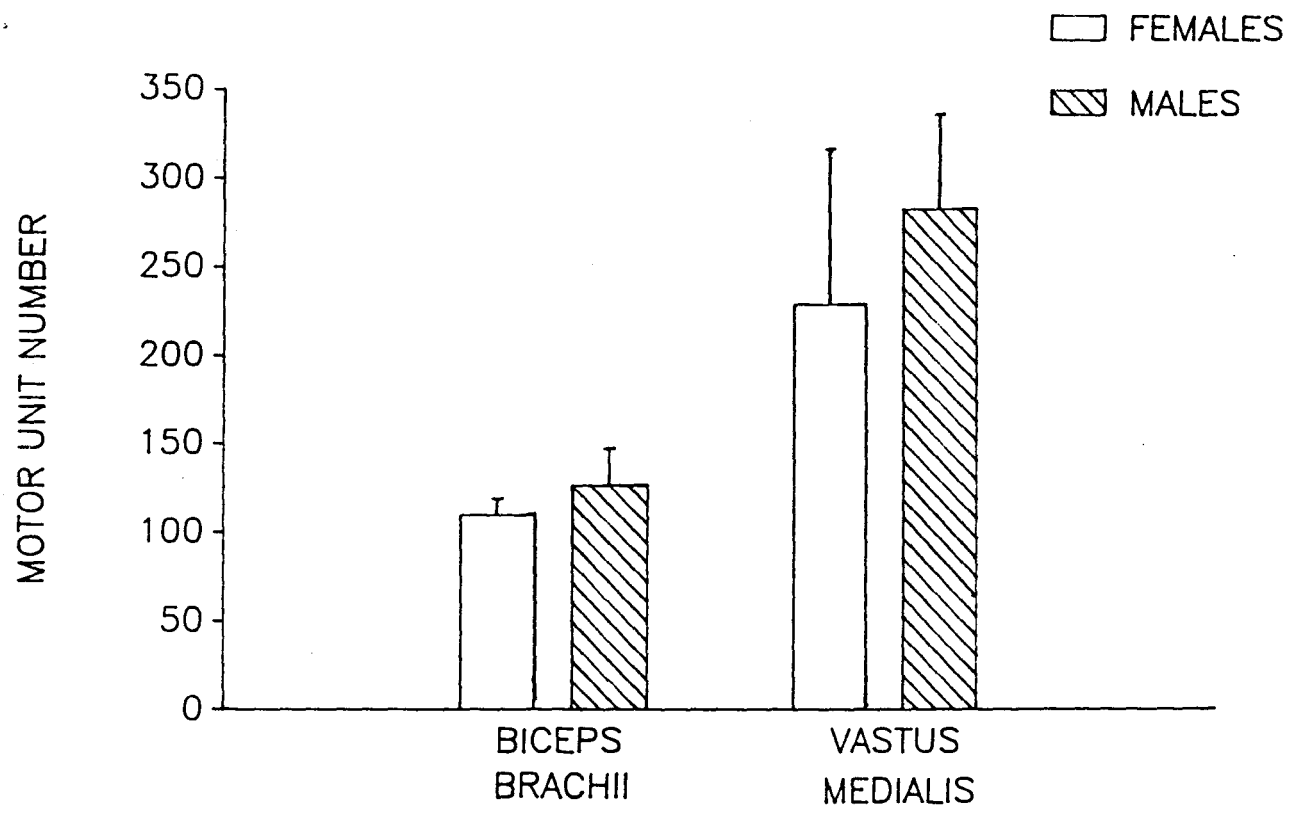

FEMALES
MALES
MOTOR UNIT NUMBER
350
300
250
200
150
100
50
0
BICEPS BRACHII
VASTUS MEDIALIS

FIGURE 22: MOTOR UNIT SIZE IN THE BICEPS BRACHII

n = 5 for females, 6 for males
Values are means $\pm$ SE

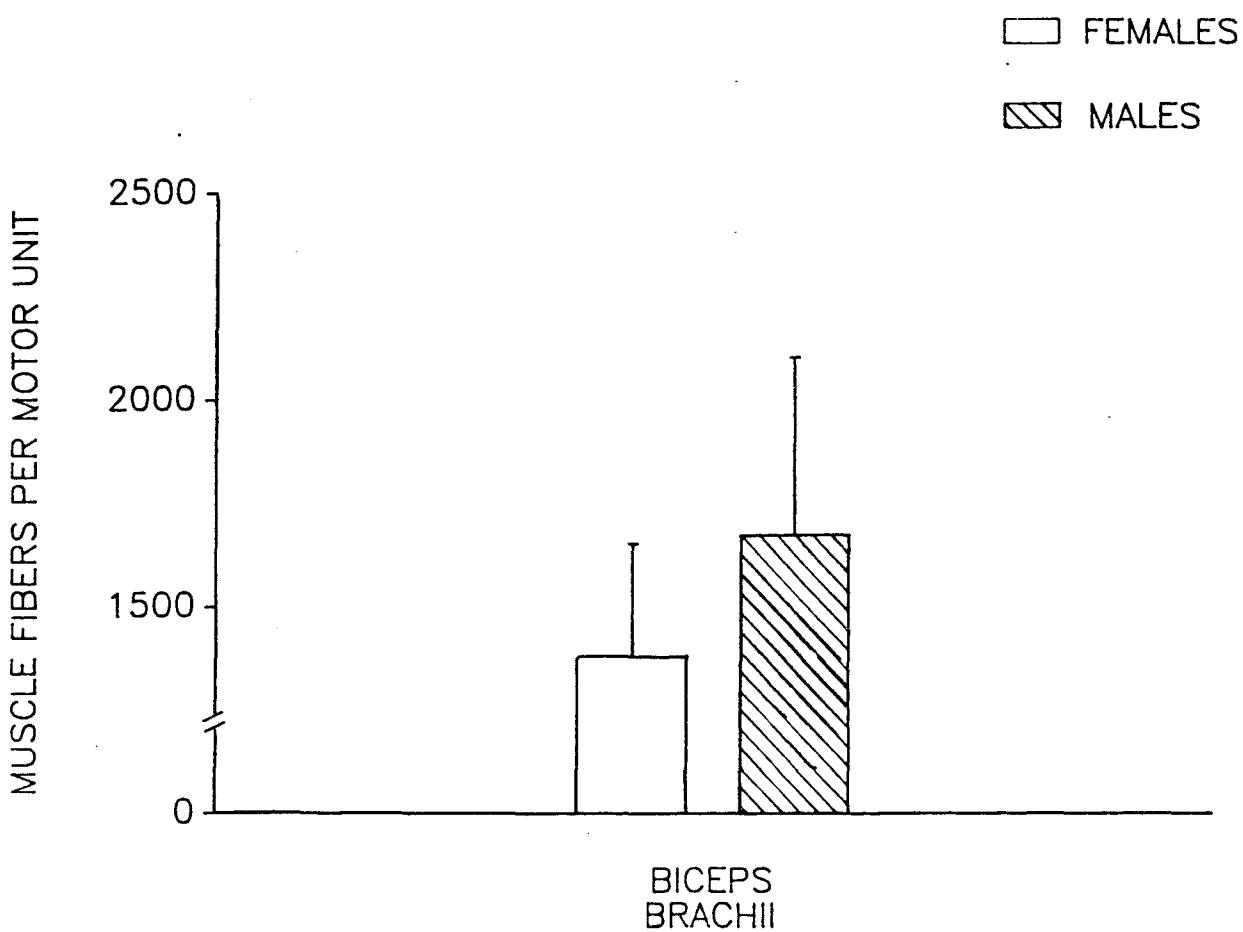
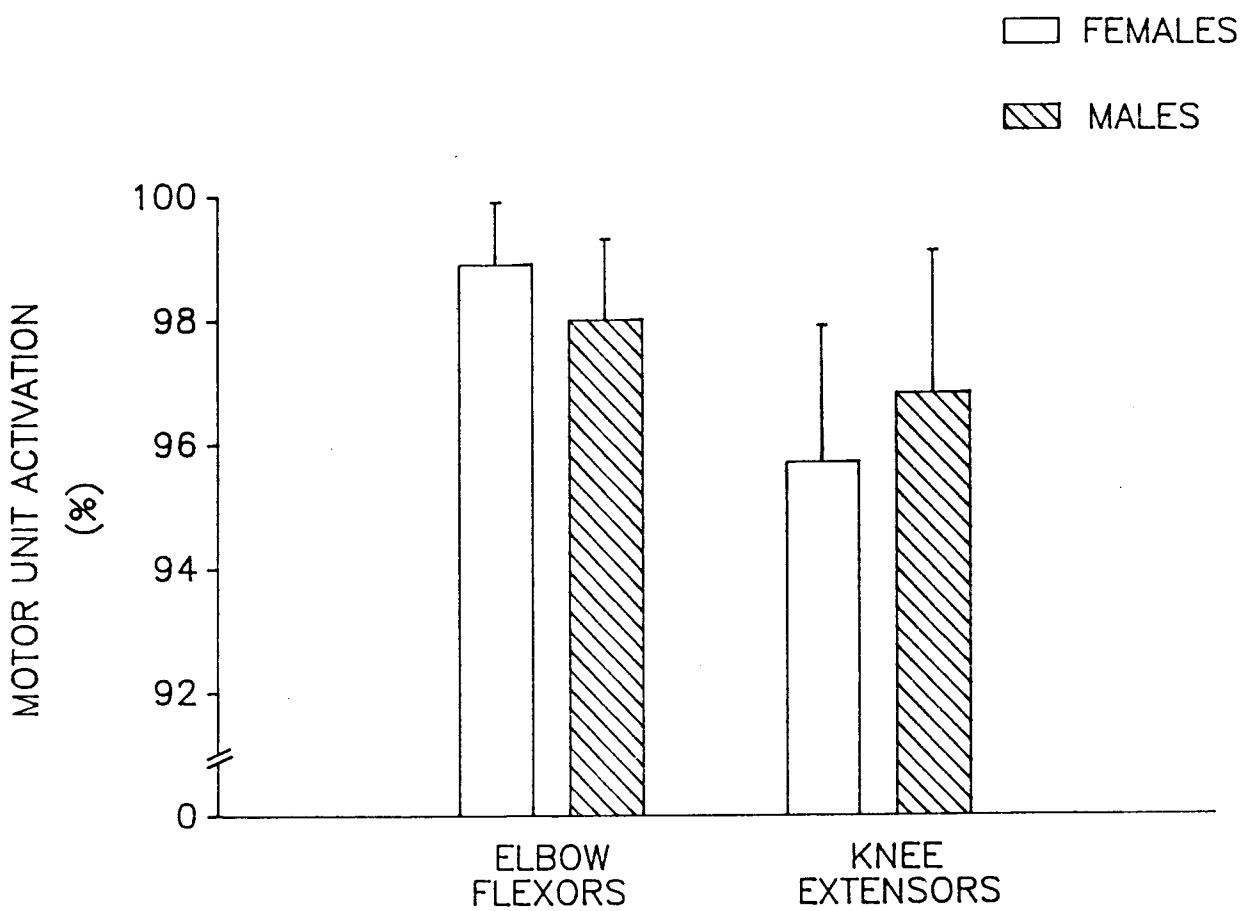

FEMALES
MALES
MUSCLE FIBERS PER MOTOR UNIT
2500
2000
1500
0
BICEPS
BRACHII

FIGURE 23: MOTOR UNIT ACTIVATION IN THE ELBOW FLEXORS AND KNEE EXTENSORS

Elbow Flexors n = 8 for females, 7 for males
Knee Extensors n = 8 for females, 6 for males
Values are means $\pm$ SE


FEMALES
MALES
MOTOR UNIT ACTIVATION (%)
100
98
96
94
92
0
ELBOW FLEXORS
KNEE EXTENSORS

vastus medialis was found between males and females (Figure 21). In addition, males and females did not differ in the number of fibers per motor unit ratio (motor unit size) in the biceps brachii (Figure 22). No significant gender difference in motor unit activation was found for the elbow flexors or knee extensors (Figure 23).

2.4 DISCUSSION

2.4.1 Voluntary Strength

The present study confirms earlier reports of a significant gender difference in upper and lower body absolute strength (Heyward et al.1976; Laubach 1976; Levine et al. 1984) (Figures 3B and 3C). When strength was expressed relative to lean body mass the males were also significantly stronger for both upper and lower body measurements, but the gender difference was more pronounced in the upper body (Figure 5D). This finding is unlike those of a number of previous studies which have found that no significant gender difference exists in lower body strength, relative to lean body mass, (Wilmore 1974; Levine et al. 1984), and agrees with that of Maughan et al. (1983). The existence of a gender difference in strength relative to lean body mass suggests the possibility of qualitative differences in male and female muscle tissue. This suggestion is not supported by the finding of the present and previous studies that no significant difference exists between the sexes in the strength to CSA ratios (Komi & Karlsson 1978; Maughan et al. 1983; Sale et al. 1987) (Figures 5A, 5B, and 5C).

The greater gender difference in upper body strength relative to lean body mass suggests differences in lean body mass distribution between the sexes. A previous study, however, has failed to find a gender difference in muscle distribution (Warren et al. 1990). Though it has traditionally been believed that females have a smaller proportion of their lean body tissue distributed in the upper body, these investigators found the arm to leg fat-free volume ratio to be similar in males and females (Warren et al. 1990). In contrast, Heyward et al. (1986) found no gender difference in upper or lower body strength when the relative distribution of lean body mass was controlled for. This finding supports the suggestion that differences in muscle distribution contribute to the greater gender difference in upper body strength expressed per kilogram lean body mass. In the present study, the ratio of elbow flexor CSA to knee extensor CSA was 25% for females and 30% for males. This finding lends further support to the suggestion that, in females, a smaller proportion of their lean tissue is distributed in the upper body.

Though not a measure of voluntary strength, evoked twitch torque is positively correlated with maximum voluntary isometric strength. The finding that a significant gender difference exists in evoked twitch torque of the elbow flexors is consistent with the gender difference in maximum voluntary isometric strength (Figure 3A), and reflects the greater muscle size of males compared to females. Though not statistically significant, the evoked twitch torque of the knee extensors was greater in the males than the

females (Figure 3A). The lack of a significant difference in this measurement probably reflects the smaller gender difference in knee extensor cross-sectional area as compared to that in the elbow flexor cross-sectional area.

2.4.2 Muscle Cross-sectional Area

The intra-observer variation in the measurement of muscle cross-sectional area was determined by the repeated measurement of a single CT scan of the vastus lateralis. The measurement was repeated 20 times. Expressed as the co-efficient of variation (CV) the intra-observer variation was 0.74%.

The mean intra-subject difference in CSA between right and left vastus lateralis and right and left biceps brachii using this technique was 5.2% and 7.9% respectively. It was assumed that the size of the vastus lateralis would not differ to a great extent between left and right sides; however, the larger intra-subject difference in left and right biceps brachii CSA may well represent biological variation between the dominant and non-dominant arms.

The finding that muscle CSA (and CSA x LL) is positively correlated to muscle strength (Figures 8-11) confirms earlier reports (Maughan et al. 1983; Maughan & Nimmo 1984; Ryushi et al. 1988). The greater CSA of the biceps brachii, vastus lateralis, elbow flexors and knee extensors in males (Figure 12) has been reported elsewhere

(Maughan et al. 1983; Ryushi et al. 1988; Alway et al. 1990), and supports the suggestion that the greater absolute strength of males is primarily the result of their larger muscle size. Unlike the present study, a gender difference in the amount of connective tissue present in the biceps has been previously reported (Sale et al. 1987). Though the males in the present study had a lower mean percentage of connective tissue in the biceps brachii, this difference was not found to be statistically significant (Figure 13). The finding that a significant gender difference exists in the proportion of connective tissue in the vastus lateralis agrees with that of Prince et al. (1977) (Figure 13). The specific tension of the muscle will be influenced by the percentage of connective tissue present since connective tissue is non-contractile and therefore does not contribute to force production. Though not measured directly, it would be expected that the strength to CSA ratio would be positively correlated with the specific tension of the muscle. While no significant gender difference in any of the strength to CSA ratios was found (Figure 5), the mean for the males was higher in all but one instance [knee extensor strength (twitch torque)/CSA x LL]. Gender differences in the amount of connective tissue found in muscle may be partially responsible for the variability in the strength to CSA ratios between the sexes.

2.4.3 Muscle Fiber Area

A. Sampling error in the determination of fiber area.

Simoneau et al. (1986) found that the variation in muscle sampling and technical procedures reached about 20-25% of the total variance (ie. total differences between subjects) in fiber area when 20 fibers of each fiber type were measured from a single biopsy sample. While Blomstrand et al. (1984) recommend the measurement of 15 to 20 fibers of each fiber type from each of two biopsy samples in the determination of fiber areas, they suggest the alternative is to measure all available fibers from a single sample. While only one biopsy sample from both the biceps brachii and vastus lateralis was obtained from each subject in the present study, it was felt that measurement of an average of 140 fibers of each fiber type would result in an acceptable sampling error.

The intra-observer variation was determined by the repeated measurement of a single muscle fiber. The measurment was repeated 20 times. Expressed as a co-efficient of variation (CV) the intra-observer variation was 3.4%.

The mean intra-subject difference in fiber areas between the right and left vastus lateralis using this technique was 16.2% for the type I fibers and 11.6% for the type II fibers ($\bar{x}$ = 13.9%). Previous studies have failed to find a significant difference in the fiber areas of the left and right vastus lateralis (Blomstrand et al.

1984; Simoneau et al. 1986). Considering that fiber area is influenced by functional demand, no attempt was made to calculate the intra-subject difference in fiber area for the right and left biceps brachii since it would be expected that greater functional demands would be placed on the dominant arm.

B. Biceps Brachii. In contrast to the finding of the present study (Figure 14), previous studies of female biceps have found the type I fibers to be larger than (Brooke & Engel 1969a) or of similar area to the type II fibers (Sale et al 1987; Alway et al. 1989). This may be due, in part, to the fact that many of the female subjects in the present study had prior exposure to resistance training which is known to cause preferential hypertrophy of the type II fibers (MacDougall et al. 1980). Moreover, although several female subjects did not have any formal resistance training history, they were involved in physical activities that may have facilitated muscle fiber growth (ie. hockey, softball, tennis). The physical activity patterns of the female subjects cannot totally explain their larger type II fibers since Alway et al. (1989) found no difference in type I and type II fiber size in the biceps brachii of female bodybuilders. It would appear, however, that the size of the type II fibers relative to the type I fibers may be dependent upon the physical activity patterns of the individual.

While the type II fiber area was approximately 80% greater than the type I fiber area in males, this difference did not achieve statistical significance (Figure 14). A significant difference in type I and type II fiber size in male biceps brachii has been reported previously (Brooke & Engel 1969a; MacDougall et al. 1982). One possible explanation for the lack of statistical significance was the wide range in type II fiber areas within the male group (range = 4488 - 18220 um^2).

Males had significantly larger type I muscle fibers than the females (Figure 14C), but despite an almost two fold difference in type II fiber size, this difference did not achieve statistical significance (Figure 14D). Again, the large variability in the size of the type II fibers in the males is one possible explanation for the lack of statistical significance. Despite the finding that males have a significantly larger mean fiber area than females (Figure 15B), fiber size appears to be dependent more on physical activity patterns than gender. Many of the females who were active in resistance training had larger mean fiber areas than males who did not weight train. The influence of biological factors can not be ruled out, however, since the largest mean fiber areas were found in males who participated in resistance training.

C. Vastus Lateralis. Consistent with previous reports, the type II fibers were larger than the type I fibers in the male vastus lateralis (Brooke & Engel 1969a; Schantz et al. 1983; Ryushi et al.

1988) (Figure 14). In contrast to a number of earlier findings, indicating that the type I fibers are larger than the type II fibers (Brook & Engel 1969a; Nygaard 1981), no significant difference in the size of the type II and type I fibers was found in female vastus lateralis (figure 14). Similar to the fiber areas in the biceps, the size of the type II fibers in the vastus lateralis of the females may reflect the activity patterns of these subjects (ie. resistance training, hockey).

Consistent with previous reports, the type II fibers of the vastus lateralis were significantly larger in the males (Schantz et al. 1983; Ryushi et al. 1988) (Figure 14D). Similar to the present study, Ryushi et al. (1988) also failed to find a significant gender difference in type I fiber area (Figure 14C). The complex interaction of biological differences between the sexes and differences in activity and training patterns may help to explain why gender differences are not always found in muscle fiber size.

2.4.5. Fiber Type Distribution

A. Sampling error in the determination of fiber type distribution. Lexell et al. (1985) recommend using 150 fibers from each of a minimum of 3 biopsy samples in order to significantly reduce the sampling error when determining fiber type distribution. There is little doubt that nonhomogeneity of muscle increased the

sampling error in the present study since only one biopsy sample was used. MacDougall et al. (1984) suggest, however, that the magnitude of such sampling errors would not be sufficient to have a systematic non-random effect on the results.

The mean intra-subject difference in fiber type distribution between the right and left biceps brachii was 21.7% for the type I fibers and 15.4% for the type II fibers. The mean intra-subject difference in fiber type distribution between the right and left vastus lateralis was 8.0% for the type I fibers and 7.0% for the type II fibers. Prior studies have found no systematic difference between the right and left vastus lateralis in fiber type distribution (Blomstrand & Ekblom 1982; Simoneau et al. 1986)

B. Biceps Brachii. The lack of a significant difference in fiber type distribution in the biceps brachii between the sexes (Figure 14A) has been reported previously (Sale et al. 1987) and supports similar findings for other muscles (Blomstrand & Ekblom 1982).

C. Vastus Lateralis. Unlike the findings of Prince et al. (1977) and Nygaard (1981), a significant gender difference in fiber type distribution and the percent type II fiber area in the vastus lateralis was found in the present study (Figure 14A). Simoneau et al. (1985) also found males had a higher percentage of type II fibers in the vastus lateralis than females. Komi and Karlsson (1978)

reported a gender difference in fiber type distribution in the vastus lateralis, however, they found males had a higher proportion of type I fibers than females. The conflicting findings of the present and previous studies may be the result of differences in the subject populations examined. The most convincing results are those of Simoneau and Bouchard (1989), in which a total of 418 biopsies were examined for gender differences in fiber type distribution. Their findings agree with those of the present study (Simoneau & Bouchard 1989).

2.4.6 Percent Type II Fiber Area and Strength/CSA Ratios

The failure of the percent type II fiber area of the biceps to correlate with any of the strength/CSA ratios of the elbow flexors (Figure 19) suggests that the specific tension of the type I and type II fibers does not differ. This is in agreement with previous findings (Sale et al. 1983; Schantz et al. 1983; Maughan & Nimmo 1984).

The positive correlation between the percent type II fiber area in the vastus lateralis and the knee extensor strength/CSA when strength was expressed as a 1RM (Figure 20C), suggests that the type II fibers have a greater specific tension than the type I fibers. This suggestion is supported by the finding of Tesch and Karlsson (1978) that a significant positive correlation exists between maximum

isometric strength of the knee extensors and the relative distribution of fast-twitch fibers. As Schantz et al. (1983) caution, however, the risk of misinterpretation is great when correlating different functional capacities to merely a qualitative measure of the muscle. A significant correlation between two variables is not necessarily inidicative of a "cause and effect" relationship. Schantz et al. (1983) found a significant positive correlation between percent type II fibers and vastus lateralis CSA; therfore, Tesch and Karlsson's (1978) data may only confirm the existence of a correlation between strength and muscle CSA and may not demonstrate a significant difference in the specific tension of the type I and type II fibers. Therefore, the correlation between percent type II fiber area and knee extensor strength (1RM) to CSA ratio found in the present study is not conclusive evidence to support the hypothesis that there exists a difference in the specific tension of type I and type II fibers. Support for this comes from the finding that the correlation between % type II fibers and the strength/CSA is not significant within each gender group. A possible alternative explanation for the present finding comes from the work of Thorstensson et al. (1976) who found that the fiber type distribution pattern of a muscle may influence the peak force of a concentric contraction, paricularily if performed at high velocities. Though not generally performed at a high velocity, the 1RM strength measurement does involve a concentric (ie. dynamic) contraction. Therefore, it could be argued that the 1RM of the knee

extensors may be influenced by the fiber type composition of the knee extensors. Additional support for this explanation comes from the finding that the fiber distribution of the vastus lateralis failed to correlate with the strength/CSA ratio when knee extensor strength was expressed as voluntary isometic (MVC) strength (Figure 20B) or twitch torque (Figure 20A).

2.4.7 Muscle Fiber Number

A. Validity of technique for estimating fiber number. The validity of the technique for estimating fiber number has been discussed in detail previously (MacDougall et al. 1984). Because of the parallel arrangement of fibers in the biceps brachii, the majority of fibers (if not all) can be expected to pass through the belly of the muscle. This is not the case for muscle of the thigh because of their pennate arrangement, thus unlike the biceps brachii, the muscle area to fiber area ratio of the vastus lateralis cannot be considered to represent fiber number. One would expect, however, a good correlation between this measure and total fiber number. The needle biopsy technique results in fully contracted tissue, therefore, fiber areas were measured with the sarcomeres in the contracted state. This results in an overestimation of fiber areas. Since the muscle CSA was measured with the sarcomeres at resting length, fiber number has been underestimated. It was felt that this would be a constant error and therefore, fiber number was not corrected for the overestimation of fiber area.

B. Reliability of technique for estimating fiber number. No evidence exists to suggest that fiber number should differ in the left and right arms. MacDougall et al. (1984) reported the mean intra-subject difference in estimated fiber number between right and left arms with this technique was 8.9% ± 3.6%. The authors suggest this difference was the result of sampling errror rather than anatomical differences.

The mean intra-subject difference in muscle area to fiber area ratio between the right and left vastus lateralis in the present study was 11.0%.

C. Biceps fiber number. One of the major findings of this study was the lack of a significant difference in the biceps fiber number between the sexes (Figure 15A). This finding is unlike those of other investigators who have reported a significant gender difference in biceps fiber number (MacDougall et al. 1983; Sale et al. 1987), but agrees with the finding of Alway et al. (1989) who failed to find a significant difference in biceps fiber number between male and female bodybuilders. This finding suggests that the greater CSA of male muscle is the result of larger fibers and not due to a greater fiber number. This suggestion is supported by the existence of a significant positive correlation between mean fiber area and biceps CSA (Figure 16A) and the lack of a correlation between fiber number and biceps CSA (Figure 16B). It is important to consider, however, that while the difference was not statistically

significant, the mean fiber number was 13% greater in males than in females and that two of the male subjects had, what appeared to be, abnormally low fiber numbers in the biceps.

C. Vastus lateralis muscle area to fiber area ratio. The finding that no significant gender difference exists in the muscle area to fiber area ratio in the vastus lateralis (Figure 17A) agrees with that of Schantz et al. (1981), however these investigators failed to correct for connective tissue and considered their results to be representative of vastus lateralis fiber number.

Again, this finding suggests that the greater mean fiber area in male vastus lateralis is responsible for their greater muscle CSA. This suggestion is supported by the significant positive correlation between vastus lateralis mean fiber area and vastus lateralis CSA (Figure 18A), and the lack of a correlation between vastus lateralis muscle area to fiber area ratio and vastus lateralis CSA (Figure 18B).

2.4.8 Motor Unit Characteristics

The present study failed to find a significant gender difference in the number of motor units in the biceps brachii and vastus medialis (Figure 21) or motor unit size in the biceps brachii (Figure 22). In addition, no significant gender difference was found in motor unit activation for either the elbow flexors or the knee

extensors (Figure 23). This finding is in agreement with that of a previous investigation (Belanger & McComas 1981) and indicates that males are no better able to maximally activate their available motor units than females.

2.4.9 Muscular Endurance

A. Elbow Flexion. The finding that a gender difference exists in the muscular endurance of the elbow flexors at a load corresponding to 60% of the 1RM (Figure 6) confirms an earlier finding (Maughan et al. 1986). Maughan et al. (1986) found that this gender difference exists for loads corresponding to 50, 60 and 70% of the 1RM but not for loads of 80 and 90%.

B. Knee Extension. No significant differences were found in the muscular endurance of the knee extensors at loads corresponding to 40 and 60% of the 1RM (Figure 7). Maughan et al. (1986) failed to find a significant gender difference in knee extension muscular endurance for forces corresponding to 50 and 80% of MVC. These authors did report, however, a significant gender difference at 20% of MVC.

From the findings of the present study and those of Maughan et al. (1986) it appears that the muscular endurance of females exceeds that of males for both isometric and dynamic exercise when the resistance represents a relatively low proportion of maximum strength.

Some disagreement exists as to the factors responsible for the gender difference in muscular endurance. Maughan et al. (1986) suggest that it may be the result of the greater potential for oxidative metabolism in the muscle fibers of females. The limiting factor in muscular endurance may be the pain and fatique associated with a decrease in intramuscular pH as a result of lactate accumulation. The ability to rely more heavily on oxidative metabolism would then delay the accumulation of lactate and, hence, exercise could be continued longer. Interestingly, however, no significant gender difference in fiber type distribution was found in the biceps brachii despite the fact that females had significantly greater muscular endurance than the males in the elbow flexors. In contrast, no significant gender difference was found in the muscular endurance of the knee extensors despite the finding that males had a significantly greater percentage of type II fibers in the vastus lateralis. These findings do not support the suggestion that the greater muscular endurance of females is the result of a greater capacity for oxidative metabolism in their muscle fibers.

During muscle contraction the intramuscular pressure may exceed the arterial blood pressure and hence, restrict adequate blood flow to the muscle involved. Mitchell et al. (1980) found that the muscle blood flow occlusion is dependent on the muscle mass involved and the absolute force developed. While both male and female subjects exercised at the same percentage of their 1RM for elbow flexion and knee extension, the absolute load lifted was greater for most of the males. As a result, males would have experienced higher

intramuscular pressures and, hence, blood flow would have been occluded to a greater extent. Differences in the degree of muscle blood flow occlusion may have influenced the gender difference in muscular endurance by enabling the females to derive a greater proportion of their energy requirements from oxidative processes.

Another explanation comes from the work of deHaan et al. (1988) who reported that differences in muscle dimensions (ie. muscle mass) between the sexes may be responsible for the gender difference in muscular endurance. These authors argue that if two muscles have similar CSAs, the longer muscle of the two will have a higher energy utilization at the same % MVC because it has a greater number of sarcomeres in series which will utilize energy but not enhance the force generated by the muscle (deHaan et al. 1988). Therefore, the metabolic cost of the exercise is dependent on muscle mass rather than just muscle CSA. The gender difference in endurance was greatest in the elbow flexors, in which there was the greatest difference in muscle mass.

Though not measured directly, it was felt that two of the male subjects had lower than average muscle development. In addition, their upper body strength measurements were the lowest in the male group. Interestingly, the muscular endurance of the elbow flexors of these two individuals was almost double that for the remainder of the male subjects. This empirical finding supports the

theories that differences in muscle occlusion forces (Mitchell et al. 1980) or differences in muscle volume (deHaan et al. 1988) may affect endurance. Therefore, gender differences in muscular endurance may be the result of differences in the muscle mass used and/or the absolute force developed and not due to a gender difference in any metabolic factors as proposed by Maughan et al. (1986)

2.5 SUMMARY

The general purpose of this study was to examine strength and skeletal muscle characteristics in males and females and to determine whether gender differences exist. Specifically, biceps fiber number was estimated to determine if males could be considered to have a "genetic advantage" over females in terms of skeletal muscle hypertrophy and growth.

Based on the results of this study the following conclusions can be made:

1. Females, on average, are approximately 65% as strong as males in the lower body and 52% as strong as males in the upper body.
2. Expressed relative to lean body mass, males are also significantly stronger in both the upper and lower body, however the gender difference is greater in the upper body.
3. Strength and muscle CSA are postively correlated.
4. Muscle CSA was greater in males than in females.
5. Male and female muscle tissue does not differ significantly in it's ability to generate force as evidenced by similar strength/CSA ratios.

6. The mean fiber area in male vastus lateralis and biceps brachii was significantly larger than that of the females.

7. No significant gender difference exists in the fiber type distribuion in the biceps brachii .

8. Males had significantly greater percentage of type II fibers than the females in the vastus lateralis.

9. No significant gender difference was found in either biceps fiber number or the muscle area to fiber area ratio of the vastus lateralis.

10. Type I and type II fibers do not appear to differ significantly in their specific tension.

11. Females have significantly greater muscular endurance in the elbow flexors at relatively light loads (60% of 1RM).

12. No significant gender difference exists in the muscular endurance of the knee extensors at loads corresponding to 40 and 60% of the 1RM.

13. No significant gender difference exists in: (i) the ability to activate the motor units of the elbow flexors or knee extensors, (ii) motor unit number in the biceps brachii or vastus medialis, or (iii) the number of fibers per motor unit in the biceps brachii.

The results of this study confirm that while qualitative differences (ie. percentage of connective tissue in muscle) and differences in limb length may influence the expression of voluntary strength in males and females, the primary factor responsible for the superior strength of adult males is their greater muscle CSA. Considering the finding that no significant gender difference exists

in biceps fiber number, it can be concluded that the greater CSA of the biceps brachii in males results from larger fibers. While the results also suggest that fiber size is influenced greatly by physical activity patterns, the role of biological influences (ie. sex hormones) must also be considered to play a major role.

While the strength potential of males and females are probably quite different due to the influence of sex hormones, it is obvious that females, on average, are further from their physiological potential than males (Simmons-Raithel 1987). The reasons for this are beyond the scope of this discussion, however, it is fair to suggest that the gender difference in strength results, in part, from behavioural as well as biological differences.

2.6 REFERENCES

Aherne, W., Ayyar, D.R., Clarke, P.A., and Walton, J.N. Muscle fibre size in normal infants, children and adolescents. An autopsy study. J. Neurol. Sci. 14: 171-182, 1971.

Alway, S.E., Grumbt, W.H., Gonyea, W.J., and Stay-Gundersen, J. Contrasts in muscle and myofibers of elite male and female bodybuilders. J. Appl. Physiol. 67: 24-31, 1989.

Alway, S.E., Stray-Gundersen, J., Grumbt, W.H., and Gonyea, W.J. Muscle cross-sectional area and torque in resistance-trained subjects. Eur. J. Appl. Physiol. 60: 86-90, 1990.

Baldwin, K. Muscle development: neonatal to adult. Exerc. Sport. Sci. Rev. 12: 1-19, 1984.

Belanger, A.Y., and McComas, A.J. Extent of motor unit activation during effort. J. Appl. Physiol. 51: 1131-1135, 1981.

Bell, R.D., MacDougall, J.D., Billeter, R., and Howald, H. Muscle fiber types and morphometric analysis of skeletal muscle in six-year old children. Med. Sci. Sports Exerc. 12: 28-31, 1980.

Bell, D.G. and Jacobs, I. Muscle fiber area, fiber type distribution and capillarization in male and female bodybuilders. Can. J. Sport Sci. 15:115-119, 1990.

Betz, W.J., Caldwell, J.H., and Ribchester, R.R. The size of motor units during post-natal development of rat lumbrical muscle. J. Physiol. 297: 463-478, 1979.

Bigland, B., and Jehring, B.J. Muscle performance in rats, normal and treated with growth hormone. J. Physiol. 116: 129-136, 1952.

Blimkie, C.J.R., Ebbesen, B., MacDougall, D., Bar-Or, O., and Sale, D. Voluntary and electrically evoked strength characteristics of obese and nonobese preadolescent boys. Hum. Biol. 61: 515-532, 1989.

Blomstrand, E., and Ekblom, B. The needle biopsy technique for fibre type determination in human skeletal muscle - a methodological study. Acta Physiol. Scand. 116: 437-442,
1982

Blomstrand, E., Celsing, F., Friden, J., and Ekblom, B. How to calculate human muscle fibre areas in biopsy samples - methodological considerations. Acta Physiol. Scand. 122: 545-551, 1984.

Bond Jr., V., Gresham, K.E., Tuckson, L.E., and Balkissoon, B. Strength comparisons in untrained men and trained women bodybuilders. J. Sports. Med. 25: 131-134, 1985.

Bouchard, C., Simoneau, J.A., Lortie, G., Boulay, M.R., Marcott, M., and Thibault, M.C. Genetic effects in human skeletal muscle fiber type distribution and enzyme activities. Can. J. Physiol. Pharmacol. 64: 1245-1251, 1985.

Brooke, M.H., and Engel, W.K. The histographic analysis of human muscle biopsies with regard to fiber types. Adult male and female. Neurology 19: 221-233, 1969.

Brooke, M.H. and Engel, W.K. The histographic analysic of human muscle biopsies with regard to fiber types. Children's biopsies. Neurology 19: 591-605, 1969.

Brown, C.H., and Wilmore, J.H. The effects of maximal resistance training on the strength and body composition of women athletes. Med. Sci. Sports Exerc. 6: 174-177, 1974.

Brozek, J., Grande, F., Anderson, J.T., and Keys, A. Densiometric analysis of body composition: Revision of some quantitative assumptions. Ann. NY Acad. Sci. 110: 113-140, 1963.

Cameron, N. The methods of auxological anthropometry. In Human Growth F. Faulkner and J.M. Tanner (eds.). Plenum Press. New York: 1978.

Close, R.J. Dynamic properties of muscle. Physiol. Rev. 52: 129-197, 1972.

Costill, D.L., Daniels, J., Evans, W., Fink, W., Krahenbuhl, G., and Saltin, B. Skeletal muscle enzymes and fiber compostition in male and female track athletes. J. Appl. Physiol. 40: 149-154, 1976.

Cureton, K.J., Collins, M.A., Hill, D.W., and McElhannon Jr., F.M. Muscle hypertrophy in men and women. Med. Sci. Sports Exerc. 20: 338-344, 1988.

Davies, J., Parker, D.F., Rutherford, O.M., and Jones, D.A. Changes in strength and cross-sectional area of the elbow flexors as a result of isometric strength training. Eur. J. Appl. Physiol. 57: 667-670, 1988.

de Haan, A., Rexwinkel, R., van Doorn, J.E., Westra, H.G., Hollander, A.P., Huijing, P.A., Woittiez, R.D., and Sargeant, A.J. Influence of muscle dimensions on economy of isometric exercise in rat medial gastrocnemius muscles in situ. Eur. J. Appl. Physiol. 57: 64-69, 1988.

Edstrom, L., and Nystrom, B. Histochemical types and sizes of fibres in normal human muscle. Acta Neurol. Scand. 45: 257-269, 1969.

Elder, G.C.B. The metabolic differentiation of human skeletal muscle during foetal and post-natal development. PhD. Dissertation: McMaster University, Hamilton, Ont. 1979.

Fahey, T.D., Rolph, R., Moungmee, P., Nagel, J., and Mortara, S. Serum testosterone, body composition, and strength of young adults. Med. Sci. Sports 8: 31-34, 1976.

Florini, J.R. Hormonal control of muscle growth. Muscle and Nerve 10: 577-598, 1987.

Fugl-Meyer, A.R. Maximum isokinetic ankle plantar and dorsal flexion torques in trained subjects. Eur. J. Appl. Physiol. 47: 393-404, 1981.

Fugl-Meyer, A.R., Eriksson, A., Sjostrom, M., and Soderstrom, G. Is muscle structure influenced by genetical or functional factors? A study of three forearm muscles. Acta Physiol. Scand. 114: 277-281, 1982.

Galea, V., Debruin, H., Cavasin, R., and McComas, A.J. The numbers and relative sizes of motor units estimated by computer. Accepted for publication. Muscle and Nerve. 1990.

Gans, C. Fiber architecture and muscle function. Exerc. Sport Sci. Rev. 10: 160-175, 1982.

Goldberg, A.L. Work-induced growth of skeletal muscle in normal and hypophysectomized rats. Am. J. Physiol. 213: 1193-1198, 1967.

Goldberg, A.L., Etlinger, J.D., Goldspink, D.F., and Jablecki, C. Mechanism of work-induced hypertrophy of skeletal muscle. Med. Sci. Sports 7: 185-198, 1975.

Goldspink, G. The proliferation of myofibrils during muscle fibre growth. J. Cell. Sci. 6: 593-603, 1970.

Gollnick, P.D., Timson, B.F., Moore, R.L., and Riedy, M. Muscular enlargement and number of fibers in skeletal muscles of rats. J. Appl. Physiol.: Respirat. Environ. Exercise Physiol. 50: 936-943, 1981.

Gomori, G.A. A rapid one-step trichrome stain. Am. J. Clin. Pathol. 20: 661-664, 1950.

Gonyea, W., Ericson, G.C., and Bonde-Petersen, F. Skeletal muscle fiber splitting induced by weight-lifting exercise in cats. Acta Physiol. Scand. 99: 105-109, 1977.

Griggs, R.C., Kingston, W., Jozefowicz, R.F., Herr, B.E., Forbes, G., and Halliday, D. Effect of testosterone on muscle mass and muscle protein synthesis. J. Appl. Physiol. 66: 498-503, 1989.

Hall-Craggs, E.C.B. The longitudinal division of fibres in overloaded rat skeletal muscle. J. Anat. 107: 459-478, 1970.

Henriksson-Larsen, K. Distribution, number and size of different types of fibres in whole cross-sections of female m tibialis anterior. An enzyme histochemical study. Acta Physiol. Scand. 123: 229-235, 1985.

Hetrick, G.A., and Wilmore, J.H. Androgen levels and muscle hypertrophy during an eight week training program for men/women. Med. Sci. Sports 11: 102, 1979.

Heyward, V.H., Johannes-Ellis, S.M., and Romer, J.F. Gender differences in strength. Res. Q. 57: 154-159, 1986.

Ho, K.W., Roy, R.R., Tweedle, C.D., Heusner, W.W., Van Huss, W.D., and Carrow, R.E. Skeletal muscle fiber splitting with weight-lifting exercise in rats. Am. J. Anat. 157: 433-440, 1980.

Holloway, J.B., and Baechle, T.R. Strength training for female athletes. A review of selected aspects. Sports Med. 9: 216-228, 1990.

Ikai, M., and Fukunaga, T. Calculation of muscle strength per unit cross-sectional area of human muscle by means of ultrasonic measurement. Int. Z. Angew. Physiol. 26: 26-32, 1968.

Jolesz, F., and Sreter, F.A. Development, innervation and activity-pattern induced changes in skeletal muscle. Ann. Rev. Physiol. 43: 531-552, 1981.

Kawai, K., Ogata, E., Takano, K., Hizuka, N., Yamashita, K., and Shizume, K. Effects of testosterone and estradiol on serum somatomedin A and growth rate of rats. Endocrinol. Jpn. 29: 435-442, 1982.

Klausen, K. Strength and weight training. In Physiology of Sports. T. Reilly, N. Secher, P. Snell and C. Williams (eds.). E. & F.N. Spon. London: 1990.

Komi, P.V., Viitasalo, J.H.T., Havu, M., Thorstensson, A., Sjodin, B., and Karlsson, J. Skeletal muscle fibres and muscle enzyme activities in monozygous and dizygous twins of both sexes. Acta Physiol. Scand. 100: 385-392, 1977.

Komi, P.V., and Karlsson, J. Skeletal muscle fibre types, enzyme activities and physical performance in young males and females. Acta Physiol. Scand. 103: 210-218, 1978.

Krahenbuhl, G.S., Archer, P.A., and Pettit, L.L. Serum testosterone and adult female trainability. J. Sports Med. 18: 359-364, 1978.

Kuhn, F.E., and Max, S.R. Testosterone and muscle hypertrophy in female rats. J. Appl. Physiol. 59:24-27, 1985.

Laubach, L.L. Comparative muscular strength of men and women: a review of the literature. Aviat. Space Environ. Med. 47: 534-542, 1976.

Layman, D.K., Hegarty, P.V.J., and Swan, P.B. Comparison of morphological and biochemical parameters of growth in rat skeletal muscles. J. Anat. 130: 159-171, 1980.

Levine, L., Falkel, J.E., and Sawka, M.N. Upper to lower body strength ratio comparisons between men and women. Med. Sci. Sports Exerc. 16: 125, 1984.

Lexell, J., Taylor, C., and Sjostrom, M. Analysis of sampling errors in biopsy techniques using data from whole muscle cross-sections. J. Appl. Physiol. 59: 1228-1235, 1985.

MacDougall, J.D., Elder, G.C.B., Sale, D.G., Moroz, J.R., and Sutton, J.R. Effects of strength training and immobilization on human muscle fibres. Eur. J. Appl. Physiol. 43: 25-34, 1980.

MacDougall, J.D., Sale, D.G., Elder, G.C.B., and Sutton, J.R. Muscle ultrastructural characteristics of elite powerlifters and bodybuilders. Eur. J. Appl. Physiol. 48: 117-126, 1982.

MacDougall, J.D., Sale, D.G., Alway, S.E., and Sutton, J.R. Differences in muscle fibre number in biceps brachii between males and females. Can. J. Appl. Sport Sci. 8: 221, 1983.

MacDougall, J.D., Sale, D.G., Alway, S.E., and Sutton, J.R. Muscle fiber number in biceps brachii in bodybuilders and

control subjects. J. Appl. Physiol.: Respirat. Environ. Exercise Physiol. 57: 1399-1403, 1984.

Maughan, R.J., Watson, J.S., and Weir, J. Strength and cross-sectional area of human skeletal muscle. J. Physiol. 338: 37-49, 1983.

Maughan, R.J., and Nimmo, M.A. The influence of variations in muscle fibre compostition on muscle strength and cross-sectional area in untrained males. J. Physiol. 351: 299-311, 1984.

Maughan, R.J., Harmon, M., Leiper, J.B., Sale, D., and Delman, A. Endurance capacity of untrained males and females in isometric and dynamic muscular contractions. Eur. J. Appl. Physiol. 55: 395-400, 1986.

Mayhew, J.L, and Gross, P.M. Body composition changes in young women with high resistance weight training. Res. Q. 45: 433-441, 1974.

McCullagh, P., Maughan, R.J., Watson, J.S., and Weir, J. Biomechanical analysis of the knee in relation to measured quadriceps strength and cross-sectional area in man. J. Physiol. 346: 60P, 1984.

Merton, P.A. Voluntary strength and fatigue. J. Physiol. 123: 553-564, 1964.

Mitchell, J.H., Payne, F.C., Saltin, B., and Schibye, B. The role of muscle mass in the cardio-vascular response to static contractions. J. Physiol. 309: 45-54, 1980.

Morris, C.B. The measurement of the strength of muscle relative to the cross-section. Res. Q. 19: 295-303, 1948

Morrow Jr., J.R., and Hosler, W.W. Strength comparisons in untrained men and trained women athletes. Med. Sci. Sports Exerc. 13: 194-198, 1981.

Motley, H.L. Comparison of a simple helium closed with the oxygen-circuit method for measuring residual air. Am. Rev. Tuber. Pul. Dis. 76: 601-615, 1957.

Narici, M.V., Roi, G.S., Landoni, L., Minetti, A.E., and Cerretelli, P. Changes in force, cross-sectional area and neural activatin during strength training and detraining of the human quadriceps. Eur. J. Appl. Physiol. 59: 310-319, 1989.

Nygaard, E. Skeletal muscle fibre characteristics in young women. Acta Physiol. Scand. 112: 299-304, 1981.

Padykula, H.A., and Herman, E. The specificity of the histochemical method of adenosinetriphosphatase. J. Histochem. Cytochem. 3:170-195, 1955.

Pope, H.G., and Katz, D.L. Affective and psychotic symptoms associated with anabolic steroid use. Am. J. Psychiatry. 145: 4-10, 1988.

Prince, F.P., Hikida, R.S., and Hagerman, F.C. Muscle fiber types in women athletes and non-athletes. Pflugers Archiv. 371: 161-165, 1977.

Purves, D. Neuronal competition. Nature 287: 585-586, 1980.

Ryushi, T., Hakkinen, K., Kauhanen, H., and Komi, P.V. Muscle fiber characteristics, muscle cross-sectional area and force production in strength athletes, physically active males and females. Scand. J. Sports Sci. 10: 7-15, 1988.

Sale, D.G., MacDougall, J.D., Alway, S.E., and Sutton, J.R. Voluntary strength and muscle characteristics in untrained men and women and male bodybuilders. J. Appl. Physiol. 62: 1786-1793, 1987.

Schantz, P., Randall-Fox, E., Norgren, P., and Tyden, A. The relationship between the mean muscle fibre area and the muscle cross-sectional area of the thigh in subjects with large differences in thigh girth. Acta Physiol. Scand. 113: 537-539, 1981.

Schantz, P., Randall-Fox, E., Hutchison, W., Tyden, A., and Astrand, P.O. Muscle fibre type distribution, muscle cross-sectional area and maximal voluntary strength in humans. Acta Physiol. Scand. 117: 219-226, 1983.

Schultz, E. Satellite cell behavior during skeletal muscle growth and regeneration. Med. Sci. Sports Exerc. 21 (suppl): S181-S186, 1989.

Simmons-Raithel, K. Are girls less fit than boys? Phys. Sportsmed. 15: 157-163, 1987.

Simoneau, J.A., Lortie, G., Boulay, M.R., Thibault, M.C., and Bouchard, C. Skeletal muscle histochemical and biochemical characteristics in sedentary male and female subjects. Can. J. Physiol. Pharmacol. 63: 30-35, 1985.

Simoneau, J.A., Lortie, G., Boulay, M.R., Thibault, M.C., and Bouchard, C. Repeatability of fibre type and enzyme activity measurements in human skeletal muscle. Clin. Physiol. 6: 347-356, 1986.

Simoneau, J.A., and Bouchard, C. Human variation in skeletal muscle fiber-type proportion and enzyme activities. Am. J. Physiol. 257 (Endocrinol. Metab. 20): E567-E572, 1989.

Tesch, P., and Karlsson, J. Isometric strength performance and muscle fibre type distribution in man. Acta Physiol. Scand. 103: 47-51, 1977.

Thorstensson, A., Grimby, G., and Karlsson, J. Force-velocity relations and fiber composition in human knee extensor muscles. J. Appl. Physiol. 40: 12-16, 1976.

Van DeGraaff, K.M. Human Anatomy. Wm. C. Brown. Iowa: 1984.

Warren, G.L., Cureton, K.J., Dengel, D.R., Graham, R.E., and Ray, C.A. Is the gender difference in peak VO2 greater for arm than leg exercise? Eur. J. Appl. Physiol. 60: 149-154, 1990.

Weibel, E.R. A stereological method for estimating volume and surface of sarcoplasmic reticulum. J. Microsc. Oxford 95: 229-242, 1972.

Westerlind, K.C., Byrnes, W.C., Freedson, R.S., and Katch, F.I. Exercise and serum androgens in women. Phys. Sportsmed. 15: 87-94, 1987.

White, T.P., and Esser, K.A. Satellite cell and growth factor involvement in skeletal muscle growth. Med. Sci. Sports. Exerc. 21 (suppl): S158-S163, 1989.

Wilmore, J.H. Alterations in strength, body composition and anthropometric measurements consequent to a 10-week weight training program. Med. Sci. Sports 6: 133-138, 1974.

Wilson, J.D. Recent studies on the mechanism of action of testosterone. New. Eng. J. Med. 287: 1284-1290, 1972.

Yamada, S., Buffinger, N., DiMario, J., and Strohman, R.C. Fibroblast growth factor is stored in fiber extracellular matrix and plays a role in regulating muscle hypertrophy. Med. Sci. Sports Exerc. 21: S173-S180, 1989.

Young, A. The relative isometric strength of type I and type II muscle fibres in human quadricep. Clin. Physiol. 4: 23-32, 1984.

Young, A., Stokes, M., and Crowe, M. The size and strength of the quadriceps muscles of old and young men. Clin. Physiol. 5: 145-154, 1985.

APPENDIX I

CORRELATION AND REGRESSION

Canadian
Academic
Technology

FILENAME: lgcsa

16 subjects
4 variables

VALUES FOR r

	vlcsa	extcs	rm
mvc	+.622	+.607	+.795
rm	+.824	+.835	
extcs	+.908		

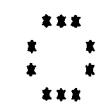
VALUES FOR r-SQUARED

	vlcsa	extcs	rm
mvc	.3874	.3684	.6318
rm	.6794	.6975	
extcs	.8253		

2-TAILED PROBABILITY VALUES
(Half this value is the 1-tailed probability)

	vlcsa	extcs	rm
mvc	.0098	.0122	.0004
rm	.0002	.0002	
extcs	.0000		

ANALYSIS OF VARIANCE



Canadian
Academic
Technology

Filename: VL#
16 subjects

CELL STATISTICS

DEP.VAR.=#v1

sex	MEAN	STAND. ERR.	STAND.DEV.	SUM SQR.	n
1	465007	41757.91	118109.2	9.764851E+10	8
2	451468.3	41528.34	117459.9	9.657777E+10	8

ANALYSIS OF VARIANCE TABLE - #v1

Source	Sum Sqr.	df	Mean Sqr.	F
sex	7.330693E+08	1	7.330693E+08	5.284028E-02
Error	1.942263E+11	14	1.387331E+10	

F (1 , 14) = 5.284028E-02 Probability = 0.80559

t = .2298701 df = 14

APPENDIX II

FIBER CHARACTERISTICS

BICEPS BRACHII				
SUBJECT	I AREA (um^2)	II AREA (um^2)	MEAN AREA (um^2)	FIBER NUMBER
FEMALES				
JS	2957	2625	2745	224,416
CH	2880	4260	3856	161,255
LB	3451	4289	3849	153,283
CM	NA	NA	2684*	NA
DS	4270	6560	5662	109,496
KA	4408	4501	4454	94,930
NJ	2079	2404	2248	204,626
SL	4339	5505	4930	150,101
MALES				
GP	3665	5240	4596	271,987
JK	4547	9847	7520	171,538
JC	3954	4501	4308	269,266
AC	5779	18220	12783	87028
YW	4960	6918	6064	98,229
XS	3263	4408	3871	178,253
JW	NA	NA	7499*	160,021
JB	6014	8238	7280	208,635

* No correction for fiber type distribution

FIBER CHARACTERISTICS CONTINUED

VASTUS LATERALIS				
SUBJECT	I AREA (um^2)	II AREA (um^2)	MEAN AREA (um^2)	MUSCLE AREA TO FIBER AREA RATIO
FEMALES				
JS	3778	2620	3224	486,973
CH	4278	5321	4887	413,342
LB	NA	NA	4467*	543,989
CM	NA	NA	4615*	394,366
DS	7644	5663	6560	347,561
KA	3011	2950	2986	626,256
NJ	3943	3645	3795	600,791
SL	NA	NA	6226*	306,778
MALES				
GP	4390	7191	6410	435,257
JK	3779	5320	4655	612,245
JC	9224	7001	7779	386,939
AC	7345	10687	9364	370,568
YW	8464	9720	9092	294,765
XS	4185	4362	4298	504,886
JW	4802	7370	6214	619,569
JB	6947	9948	8748	386,517

* No correction for fiber type distribution

FIBER TYPE DISTRIBUTION

SUBJECT	BICEPS BRACHII		VASTUS LATERALIS	
	% TYPE I	% TYPE II	% TYPE I	% TYPE II
FEMALES				
JS	36.1	63.9	52.2	47.8
CH	29.3	70.7	41.6	58.4
LB	52.5	47.5	NA	NA
CM	NA	NA	NA	NA
DS	39.2	60.8	45.3	54.7
KA	50.6	49.4	59.7	40.3
NJ	47.7	52.3	50.4	49.6
SL	49.3	50.7	NA	NA
MALES				
GP	40.9	59.1	27.9	72.1
JK	43.9	56.1	43.1	56.9
JC	35.1	64.7	35.0	65.0
AC	43.7	56.3	39.6	60.4
YW	43.6	56.4	NA	NA
XS	50.4	49.6	35.9	64.1
JW	NA	NA	45.0	55.0
JB	43.1	56.9	40.0	60.0

MOTOR UNIT CHARACTERISTICS

SUBJECT	BICEPS BRACHII		VASTUS MEDIALIS
	NUMBER	SIZE	NUMBER
FEMALES			
JS	NA	NA	117
CH	126	1280	NA
LB	126	1217	143
CM	123	NA	164
DS	90	1217	NA
KA	121	785	NA
NJ	85	2407	490
SL	NA	NA	NA
MALES			
GP	192	1417	109
JK	NA	NA	NA
JC	75	3590	277
AC	179	486	465
YW	83	1116	161
XS	NA	NA	NA
JW	83	1928	318
JB	139	1501	362

MUSCLE CROSS-SECTIONAL AREA

SUBJECT	BICEPS BRACHII (cm^2)	TOTAL FLEXORS (cm^2)	VASTUS LATERALIS (cm^2)	TOTAL EXTENSORS (cm^2)
FEMALES				
JS	7.7	14.5	21.2	50.5
CH	7.5	17.6	24.8	63.9
LB	7.3	18.8	30.9	73.1
CM	NA	NA	22.4	77.4
DS	7.6	18.1	26.0	74.5
KA	5.1	13.8	23.4	60.1
NJ	5.4	12.1	27.1	74.0
SL	8.8	18.8	22.9	67.0
MALES				
GP	14.6	27.4	32.7	90.7
JK	15.0	27.1	34.0	80.5
JC	13.0	25.0	35.3	96.0
AC	12.5	31.0	40.5	94.5
YW	7.3	20.5	31.3	85.5
XS	8.7	19.4	26.2	67.4
JW	13.7	35.5	45.6	106.6
JB	17.2	32.3	38.4	98.6

STRENGTH AND MUSCULAR ENDURANCE

SUBJECT	SINGLE ARM			
	MVC (N•m)	TWITCH TORQUE (N•m)	1RM (kg)	REPS 40% of 1RM
FEMALES				
JS	28.1	3.2	8.0	14
CH	35.1	3.7	8.5	42
LB	48.6	6.3	11.75	53
CM	49.1	5.3	8.75	41
DS	46.5	5.1	14.0	50
KA	29.7	2.5	10.5	NA
NJ	37.1	5.2	8.0	32
SL	42.8	5.1	11.25	31
MALES				
GP	91.3	14.4	23.0	16
JK	70.8	5.6	17.5	17
JC	93.4	11.0	20.0	14
AC	74.4	7.9	21.75	13
YW	49.6	7.5	10.5	27
XS	57.7	7.3	10.5	31
JW	96.6	10.0	26.0	16
JB	76.3	12.2	24.75	37

STRENGTH AND MUSCULAR ENDURANCE

SUBJECT	SINGLE LEG			
	MVC (N•m)	TWITCH TORQUE (N•m)	1RM (kg)	REPS 40/60% of 1RM
FEMALES				
JS	177.9	19.4	20.0	13/7
CH	278.1	52.8	35.0	14/10
LB	184.1	35.3	30.0	11/9
CM	207.2	42.1	33.0	12/7
DS	145.1	24.0	24.5	17/10
KA	140.9	26.2	15.0	NA/7
NJ	169.5	34.9	32.25	16/10
SL	135.9	24.9	30.0	15/9
MALES				
GP	342.0	55.6	44.5	13/10
JK	262.5	37.4	42.25	10/7
JC	320.7	42.2	50.0	5/4
AC	291.5	66.1	55.0	15/9
YW	133.7	38.5	22.25	15/9
XS	213.2	27.4	30.0	13/5
JW	289.4	49.0	52.0	11/4
JB	243.1	34.6	60.0	14/9

APPENDIX III

McMASTER UNIVERSITY
HAMILTON, ONTARIO, CANADA

COMMITTEE ON
THE ETHICS OF RESEARCH ON HUMAN SUBJECTS

TO: The Office of Research Services

RE: Dr. J.D. MacDougall

TITLE: Strength and Muscle Characteristics of Untrained Males and Females

The above named applicant has submitted an application to the Committee on Ethics of Research on Human Subjects.

The Committee has reviewed this request and finds that it meets our criteria of acceptability on ethical grounds. The review has been conducted with a view toward insuring that the rights and privacy of the subject have been adequately protected; that the risks of the investigation do not outweigh the anticipated gain; and that informed consent will be appropriately obtained.

We concur in all necessary endorsements of the application.

S. Martin Taylor

Date: 18 April 1990

For the Committee on the Ethics of Research on Human Subjects

C.K. Bart, Associate Professor, Business
T. Beckett, Judge, Unified Family Court
B. Donst, Ecumenical Chaplain, Chaplains' Office
D. Elliott, Associate Professor, Physical Education and Athletics
J. Gaa, Associate Professor, Business
T. Kroeker, Lecturer, Religious Studies
R. Milner, Associate Professor, Clinical Epidemiology and Biostatistics
R.J. Preston, Professor, Anthropology
J. Synge, Associate Professor, Sociology
S.M. Taylor, Professor, Geography (Chairman)

INFORMATION AND CONSENT FORM

The principal investigator for this project is Andrea Miller. She will explain to you in detail the procedures involved in this study. In addition, you are asked to carefully read the following information form and sign it if you wish to participate as a subject in this study.

A. PURPOSE

The purpose of this investigation is to examine various muscle characteristics in the biceps brachii (upper arm) and vastus lateralis (thigh) in both males and females so that we may better understand the factors responsible for the greater muscle strength of adult males.

B. PROCEDURE

This investigation will require participation by the subject over 3 separate days. A total of approximately 7-8 hours will be required to complete the entire experimental protocol. The following measurements will be made using non-invasive techniques involving minimal or no risk to the subject: height, weight, bone length, muscle twitch characteristics, maximum voluntary strength, muscular endurance, lean body mass and motor unit characteristics.

In addition to the above, muscle and bone cross-sectional area will be measured by a computerized tomographic scan and muscle fiber characteristics (number and size) will be determined using a small sample of muscle tissue from the biceps and vastus lateralis extracted using a sterile hollow needle (needle biopsy technique).

C. POSSIBLE RISKS

CT Scan

CT scans will be taken of the upper arm and mid-thigh on one side only. In order to correctly determine maximum muscle cross-sectional area, three 5-10mm width scan will be taken for both the upper arm and thigh (one at the estimated point of greatest CSA, one above this point and one below it). The CT scan is a relatively safe procedure, however it does involve exposure to radiation. The exposure level is approximately one-tenth the level of conventional x-ray procedures and considerably below the annual acceptable limit set for members of the public. The above sites can be scanned without exposing reproductive organs to direct radiation.

Needle Biopsy

This procedure involve the local injection of an anaesthetic (freezing) into the skin after which a small (4mm) incision will be made and a small (50-100mg) piece of muscle removed with a special needle. After the procedure a suture will close the incision and pressure will be applied to minimize bruising. Most people report little discomfort with the procedure. It will be performed by a physician who is familiar with the technique.

Complications with the procedure are rare. In our experience with athletes, less than 1 in 400-500 subjects experience a local skin infection, 1 in 30-40 have a temporary (up to 4 months) localized loss of sensation in the skin at the incision site, and a few subjects have mild bruising around the site for 4-5 days. There is also the very rare chance (1 in one million) that you may be allergic to the local anaesthetic.

D. CONFIDENTIALITY OF RESULTS

The data collected will be used in the preparation of a Master of Science degree thesis. Subjects will not be identified by name in the write-up or in any subsequent reports resulting from this investigation.

E. RENUMERATION

You will receive an honourarium of $100.00 to help compensate you for your time committment and travelling expenses.

F. FREEDOM TO WITHDRAW FROM THE STUDY

You are free to withdraw from the study at any time. Only subjects who complete the entire experimental protocol will receive renumeration.

I have read and understand the above explanation of the purpose and procedures of this investigation and agree to participate as a subject.

_____ _____

Signature Witness

_____

Date