THE EFFECTS OF TRAINING AND IMMOBILIZATION UPON NEUROMUSCULAR FUNCTION IN MAN

By

DIGBY G. SALE, B.P.H.E., M.A.

A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfilment of the Requirements
for the Degree
Doctor of Philosophy

McMaster University
February 1979

ADAPTATION TO TRAINING AND IMMOBILIZATION IN MAN

DOCTOR OF PHILOSOPHY (1979)
(Medical Sciences)

McMASTER UNIVERSITY
Hamilton, Ontario

TITLE: Effects of Training and Immobilization Upon Neuromuscular Function in Man.

AUTHOR: Digby G. Sale, B.P.H.E. (University of Toronto)
M.A. (University of Western Ontario)

SUPERVISOR: Professor A. J. McComas

NUMBER OF PAGES: xvii, 366

ABSTRACT

The effects of strength training and immobilization upon neuromuscular function in man were investigated. The selected measures of neuromuscular function were voluntary strength and a number of electrophysiological measurements, including motor unit counts, motor nerve conduction velocity, reflex potentiation, and the contractile properties of isometric twitch contractions.

Three kinds of experiments were conducted. First, subjects participated in training and immobilization experiments. Training, which consisted of maximal isometric and concentric muscle contractions and weight lifting, was performed three times per week over a period of 10-20 weeks. Relative disuse of selected muscle groups was achieved by immobilizing the elbow, wrist and thumb joints in a cast for 5-6 weeks. Second, measurements were made in selected groups of athletes (weight lifters, gymnasts, cyclists, sprinters, cross country skiers) to provide cases of long term training. Third, measurements were made on control subjects, whose results were compared to those of the athletes.

Training resulted in an increase in voluntary strength. As cases of long term training, voluntary strength was enhanced in weight lifters and cyclists. Immobilization resulted in a decrease in voluntary strength.

Training had no effect upon motor unit counts and the motor unit counts in the weight lifters were normal; however, the gymnasts exhibited reduced motor unit counts in distal but not proximal muscles. It was hypothesized that injury to the nerves at the wrist and ankles was

responsible for the reduced motor unit counts in the gymnasts. Immobilization had no effect upon motor unit counts.

Neither training nor immobilization caused a change in motor nerve conduction velocity in relation to the control condition; however, in one group of subjects, there was a small though significant difference between the greater post training and the lesser post immobilization values. Nerve conduction velocity was greater in weight lifters and gymnasts than in controls.

Reflex potentiation increased following training, providing new evidence in support of the hypothesis that adaptation occurs within the nervous system in response to training. In agreement with the above finding was the enhanced reflex potentiation in the weight lifters. Immobilization caused a decrease in reflex potentiation, indicating that the nervous system is involved in the adaptation to relative disuse as well as to training.

Muscle (triceps surae) twitch tension and contraction time were greater in weight lifters than in controls. In this same muscle, short term training resulted in an increase in twitch half relaxation-time. These findings represent the first report of a slowing of muscle contraction in response to training.

In conclusion, the present investigation provided new evidence indicating adaptation within both the muscle and the nervous system in response to strength training and within the nervous system in response to immobilization.

ACKNOWLEDGEMENTS

I wish to thank Dr. A. J. McComas for his enthusiasm, encouragement and advice throughout the preparation of this thesis. Gratitude is also expressed to Dr. M. Rathbone and Dr. J. D. MacDougall for their advice and suggestions. I wish also to thank Dr. A. R. M. Upton for his advice and helpful suggestions.

I also thank Mr. Glen Shine and Mr. John Moroz for their technical assistance and Ms. Phyllis Koetting for typing the thesis.

CONTENTS

LIST OF FIGURES

Figure Page

LIST OF TABLES

Table Page

I. INTRODUCTION

A. General Introduction

Purpose of the Investigation

The purpose of the present investigation was to observe the effects of strength training and immobilization upon neuromuscular function in man. The measures of neuromuscular function selected for the investigation were voluntary strength and a number of electrophysiological measurements, including motor unit counts, motor nerve conduction velocity, reflex potentiation, and the contractile properties of isometric twitch contractions. The basis for selecting these measures is presented in the conclusion to the introduction, following the review of the literature.

The term "voluntary strength" refers to the mechanical effect of a maximal voluntary muscle contraction. Voluntary strength may be measured as the peak force (or torque) developed during a contraction, or as impulse (force x time), average force (impulse/time), work (force x displacement) and power (work/time).

The term "strength training" refers to the regular performance of forceful muscle contractions (e.g. lifting heavy weights) in order to increase voluntary strength. The term "immobilization" in the present investigation refers to fixation (mechanically preventing movement at a joint) of a joint by means of a cast.

Scope of the Investigation

To fulfill the purpose of the investigation, three kinds of experiments were conducted. First, healthy, untrained subjects participated in training and immobilization experiments. Measurements were made before and after immobilization and training. Second, measurements were made in selected groups of athletes. Weight lifters and gymnasts received special attention because these athletes require a high level of voluntary strength for successful performance. The other groups of athletes included cyclists, cross country skiers and sprinters. Third, measurements were made on healthy control subjects. The results in the control subjects provided a basis for comparison with the groups of athletes, as well as being of interest by themselves. Control experiments were also conducted to establish the reproducibility of the measurements.

The training and athlete experiments were complementary to one another. A limitation of the training experiments was the short duration (10-20 weeks) of the training periods, while the athletes provided cases of long term training (several years). However, in any comparison among groups of athletes or between athletes and controls, the question arises as to what extent the observed differences were due to training or genetic endowment. The training experiments served to demonstrate whether training could account in part for the observed differences.

The training and immobilization experiments were also complementary to each other. The effects of training represent neuromuscular adaptation to greater than normal function and the effects of immobilization represent adaptation to less than normal function. Thus, the training and immobilization conditions permitted observation of adaptation in opposite directions from the normal condition.

B. Review of Literature

Introduction

The effects of training and immobilization upon the morphology, biochemistry and contractile properties of muscle have been the subjects of human and animal experiments for many years. The effects of training and immobilization upon the nervous system have received less attention, although it has long been suspected that the nervous system plays a role in the adaptation to strength training (e.g. Delorme et al, 1950).

There are at least three reasons for the sustained popularity of training and immobilization experiments. First, these two conditions, because of their opposing nature, provide an excellent model for investigation of the fundamental process of cellular adaptation. Second, the knowledge obtained about the regulation of function in normal tissue might lead to further understanding of the response of tissue to disease. Third, the results of these investigations may find application in rehabilitation medicine and athletic training.

Below, the current knowledge of the effects of strength training and immobilization upon neuromuscular function in man and animals will be reviewed. The review will be delimited. The effects of endurance training will not be reviewed in detail (for references, see Hollozy, 1975 and Hollozy & Booth, 1976). In some animal experiments, a condition similar to strength training has been induced by denervation or tenotomy of synergistic muscles; thus, the remaining functionally intact muscle(s) is(are) subjected to functional overload. The most relevant of these studies will be reviewed. The review of the effects of immobilization will be restricted primarily to investigations that have employed joint fixation by means of casts as the model for relative "disuse". Other models have included denervation and tenotomy. These and other models of disuse have been recently reviewed by McComas (1977, pp. 82-88). Some of the difficulties of interrelating the findings from experiments using cast immobilization, denervation and tenotomy as models for disuse have also been discussed by Booth and Kelso (1973b).

Effects of Training

Voluntary Strength

In Man

The current methods of strength training are isometric exercise, weight training and isokinetic exercise (for a recent review of these methods, see Lamb, 1978, pp. 135-139). Isometric exercise involves performing maximal or near maximal isometric contractions (muscle remains at the same length while producing tension) for a few seconds. Weight training involves raising and lowering weights against the force of gravity. In raising the weight, muscles perform a concentric contraction (muscles shorten while producing tension) while in lowering the weight the muscles perform an eccentric contraction (muscles lengthen while producing tension). The term "isotonic" is often applied to weight training exercise; however, the application is incorrect. "Isotonic" means "same tension" but the concentric and eccentric contractions of weight lifting are rarely if ever isotonic (Astrand & Rodahl, 1977, p. 103). In fact, isometric contractions are more likely to be isotonic. The term "isokinetic" is relatively recent (Perrine, 1968) and means "same velocity". An isokinetic device allows maximal concentric or eccentric contractions to be performed at a preset constant velocity. Theoretically, isometric contraction is a special case of isokinetic contraction, in which the velocity is zero. It is not intended here to discuss the relative merits of the different methods of strength training; however this subject has been reviewed by Clarke (1973) and Rasch (1974).

Regardless of the method of training, two general principles of strength training are applied. First, the training should involve muscle contractions of maximal or near maximal force (Muller, 1970). In isometric and isokinetic training, maximal or near maximal muscle contractions are performed. In weight training, weights are selected which permit the performance of a few repetitions (consecutive lifts) only before fatigue occurs. This approach to weight training has been called heavy resistance, low repetition exercise, while endurance may be trained by performing low resistance, high repetition exercise (Delorme, 1945). The second principle of training is progression. As strength increases, the training load must be progressively increased (Hellebrand & Houtz, 1956). In isometric and isokinetic training, progression is achieved automatically as the trainee continues to perform maximal voluntary contractions during the course of training. In weight training, progression is achieved by lifting progressively heavier weights as strength increases.

It is well documented that strength training does in fact significantly increase voluntary strength. Isometric training (e.g.

Darcus & Salter, 1955; Grimby et al, 1973a,b; Hettinger & Muller, 1953; Komi & Buskirk, 1972; Mathews & Kruse, 1957; Muller, 1962, 1970), isokinetic training (e.g. Komi & Buskirk, 1972; Mannheimer, 1969; Moffroid & Whipple, 1970; Moffroid et al, 1969; Pipes and Wilmore, 1975; Thistle et al, 1967) and weight training (e.g. Berger, 1960; Delorme et al, 1952; Pipes & Wilmore, 1975; Rasch & Morehouse, 1957; Stromme et al, 1974; Tanner, 1952; Thorstennson et al, 1976b; Wilmore, 1974) have all proven effective for increasing voluntary strength. Generally, strength increases by a few per cent per week for the first several weeks of training (Clarke, 1973; Muller, 1962, 1970). The most common training response is one of a gradually decreasing rate of strength increase (Berger, 1960; Gray, 1966; Muller, 1962, 1970). When the same training programme is administered to a group of subjects, the individual variation in response is large (Berger, 1960; Brown & Wilmore, 1974; Craikes, 1957; Gray, 1966; Mathews & Kruse, 1957; Jones, 1966; Rose et al, 1957). For example, Berger (1960) found a range in the individual training increase from 12-48% after weight training while Jones (1966) observed a range of -8% to 129% in the individual isometric training increase. It has also been observed that the response to training varies in different muscle groups and that the variation is due in part to the variation in the initial strength of the muscle groups, expressed as a proportion of the maximum attainable strength (Hettinger & Muller, 1953; Muller, 1962).

In Animals

It is more difficult to gain the co-operation of animals in voluntary strength training experiments; nevertheless, an increase in weight lifting performance by training has been demonstrated in the rat (Gordon et al, 1967b), mouse (Goldspink, 1964), hamster (Goldspink & Howells, 1974), cat (Gonyea & Ericson, 1976) and the Lesser Bushbaby (Edgerton, 1976). An increase in strength by isometric training has been demonstrated in the rat (Exner et al, 1973 a, b).

Muscle

1. Contractile Properties

In Man

The term "contractile properties" refers to the twitch tension, tetanic tension, contraction time, half relaxation time and rate of tension development of muscle contractions (usually isometric) evoked by artificial nerve stimulation rather than voluntary control. Liberson & Asa (1959) observed the effect of twelve weeks of isometric and weight training upon the twitch tension of the hypothenar muscles (i.e. abduction of the fifth digit). Training caused a 60% increase in twitch tension and a 150% increase in voluntary strength. No other contractile properties were investigated. These authors interpreted the difference in training increase between twitch tension and voluntary strength as indicating that extramuscular adaptation to training occurred. However, the observed difference might have been smaller if tetanic rather than twitch tension had been measured (see below). To the author's knowledge, this is the only investigation that has observed the effects of strength training upon the contractile properties of human muscle.

In Animals

(1) Twitch and Tetanic Tension. Twitch tension has been shown

to increase in the flexor carpi radialis and palmaris longus of the cat (Gonyea & Bonde-Petersen, 1978) but to remain unchanged in the gastrocnemius of the Lesser Bushbaby (Edgerton, 1976) after weight training. In both of these studies, there was a significant increase in tetanic tension. Isometric training resulted in an increase in tetanic tension of rectus femoris but not soleus of the rat (Exner et al, 1973a, b). In contrast, endurance training apparently does not affect twitch or tetanic tension (Barnard et al, 1970; Edgerton et al, 1972).

The findings of Edgerton (1976) are of interest, for they show that training intense enough to cause a significant increase in tetanic tension failed to cause a significant increase in twitch tension. These results encourage the interpretation that tetanic tension is a more sensitive indicator than twitch tension of increased contractile strength in muscle after training.

A model that has been used to simulate strength training consists of overloading a muscle by functionally eliminating its synergist(s). Twitch tension (Binkhorst & van't Hof, 1973) and tetanic tension (Binkhorst, 1969; Binkhorst & van't Hof, 1973; Van Linge, 1962) increased in rat plantaris following denervation of synergists. Tenotomy of synergists resulted in an increase in twitch and tetanic tension in the soleus of the cat (Jewell & Zaimis, 1954) and an increase in the tetanic tension of mouse soleus (Rowe, 1969).

<u>(2) Contraction Time, Half Relaxation Time and Rate of Tension Development</u>. Gonyea & Bonde-Petersen (1978) observed an increase in twitch contraction and half relaxation time and a decrease in rate of tetanic tension development in the flexor carpi radialis/and palmaris

longus of the cat after weight training, while Edgerton (1976) observed no significant changes in these measures in the gastrocnemius of the Lesser Bushbaby after weight training. It has been suggested that the difference in results between these two investigations may be related to a difference in the intensity or duration of training (Gonyea & Bonde-Petersen, 1978). Exner et al (1973a) found an increase in twitch contraction time in soleus and a decrease in contraction time in rectus femoris of the female rat after isometric training; in the male rat, the same training programme had no effect on these measures (Exner et al, 1973b).

The overloading of a muscle by functional elimination (denervation, tenotomy, excision) of synergists has resulted in an increased twitch contraction time in both fast (Gutmann et al, 1969, 1970, 1971; Gutmann & Hajek, 1971; Vrbova, 1963) and slow (Gutmann et al, 1971; Rowe, 1969) muscles. Overloading muscles of one limb by deafferenting (severance and removal of dorsal roots) the contralateral limb resulted in an increased contraction time of the overloaded muscles in the cat (Olson & Swett, 1969). On the other hand, Binkhorst (1969) and Binkhorst & van't Hof (1973) observed no change in contraction time in rat plantaris after denervation of synergists.

Half relaxation time has been shown to increase in fast (Gutmann & Hajek, 1971; Gutmann et al, 1970, 1971) and slow (Gutmann et al, 1971) muscles after functional elimination of synergists.

Barnard et al (1970) and Edgerton et al (1972) found no change in twitch contraction or half relaxation time after endurance training in the guinea pig and Lesser Bushbaby respectively, while Gutmann & Hajek (1971) observed a decrease in contraction and half relaxation time in the rat after intensive swimming exercise.

2. Muscle Size

In Man

In human strength training experiments, changes in gross muscle size have usually been measured as changes in limb girth. An increase in voluntary strength after strength training has often been accompanied by an increase in limb girth (Barney & Bangerter, 1961; Delorme et al, 1952; Hettinger & Muller, 1953; MacDougall et al, 1977b; McMorris & Elkins, 1954; Marley, 1962; Meyers, 1967; O'Shea, 1966; Pencek, 1966; Pipes & Wilmore, 1975; Rasch & Morehouse, 1957; Stromme et al, 1974; Tanner, 1952; Ward, 1963; Wilmore, 1974). However, increases in voluntary strength without significant increases in limb girth have also been reported (Liberson & Asa, 1959; Penman, 1970; Rose et al, 1957; Tanner, 1952; Thorstensson et al, 1976b; Wilmore, 1974).

Apparently, it is more difficult to develop muscle size in the legs and especially the calves than in the arms (Delorme et al, 1952; Fahey & Brown, 1973; Pipes & Wilmore, 1975; Stromme et al, 1974; Tanner, 1952; Ward, 1963; Wilmore, 1974). The experimental results cited are in agreement with the empirical observations of body building authorities (Fallon & Saunders, 1960, p. 91; Franz, 1969, p. 16; Kirkley, 1963, p. 36; O'Shea, 1976, p. 58; Rader, 1956, p. 26; Rasch, 1975, p. 44; Richford, 1968, p. 21; Steiner, 1974, p. 67).

It is interesting to note that body builders prefer weight training over isometric training for increasing muscle size; in fact, they usually avoid isometric training (Gordon et al, 1967c; MacQueen, 1954; Richford, 1966, p. 9). There is some experimental evidence to support this custom (Marley, 1962; Rasch & Morehouse, 1957; Ward, 1963). The avoidance of isometric exercise by the most earnest and successful body builders may be surprising to those(including muscle physiologists) who have been exposed to "Charles Atlas" and "Bullworker" advertisements. The misconception is due in part to the fact that some successful weight trained body builders sell their services to the advertisers of isometric training equipment.

Also of interest is the distinction which body builders and competitive weight lifters make between weight training for strength and weight training for muscle size. Thus, competitive weight lifters use very heavy weights in sets of very low (1-3) repetitions, while body builders use lighter weights in many sets of higher (6-10 or more) repetitions (Homola, 1968, p. 17; Kirkley, 1963, p. 11; Lamb, 1978, p. 151; MacQueen, 1954; Rasch, 1975, p. 2; Richford, 1966, p. 16).

In summary, there is evidence that in some cases, increased voluntary strength after training is associated with an increase in muscle size. Presumably, the increase in muscle size is the result of anatomical changes in the muscle that could account in part for the increase in voluntary strength (see below).

In Animals

In animal experiments, changes in gross muscle size after training have usually been measured as changes in muscle weight. Weight training has caused an increase in muscle weight in the cat (Gonyea & Bonde-Petersen, 1978; Gonyea & Ericson, 1976; Gonyea et al, 1977) and the Lesser Bushbaby (Edgerton, 1976) but no increase in muscle weight in the mouse (Goldspink, 1964) or rat (Gordon et al, 1967b). The increase in muscle weight has been associated with an increase (Gonyea & Bonde-Petersen, 1978) and no change (Edgerton, 1976) in twitch tension, an increase in tetanic tension (Edgerton, 1976; Gonyea & Bonde-Petersen, 1978), and an increase (Gonyea & Bonde-Petersen, 1978) and no change (Edgerton, 1976) in contraction and half relaxation time.

In contrast, endurance training does not increase muscle weight in the guinea pig (Barnard et al, 1970), Lesser Bushbaby (Edgerton et al, 1972) and rat (Gordon, et al, 1967a); nor is there any change in contractile properties (Barnard et al, 1970; Edgerton et al, 1972).

There are other training studies which are difficult to classify as involving strictly endurance or strength training. Staudte et al (1973) found that "sprint" training in the rat resulted in no change in weight of soleus and rectus femoris; in both muscles, there was an increase in tetanic tension, and in soleus there was a decrease in contraction time. This latter finding was in contrast to the increase in soleus contraction time found after isometric training (Exner et al, 1973a). Seiden (1976) observed an increase in the weight of extensor digitorum longus (EDL) of the rat after swimming exercise. Gutmann & Hajek (1971) found no change in the weight of rat EDL and soleus after swimming exercise; however, there was a decrease in contraction time.

In summary, if the strength training model in the cat (Gonyea & Ericson, 1976) were taken as the most successful, and if the studies by Barnard et al (1970) and Edgerton et al (1972) were taken as representative of definite endurance training, then it can be concluded that strength training results in an increase in muscle size and strength and an increase in contraction and half relaxation time while endurance training causes no change in these measures. Training which falls between these extremes produces variable results.

An experimental model that has been associated with strength training (Goldberg et al, 1975) is the model often referred to as "compensatory hypertrophy" (e.g. Gutmann et al, 1970; Mackova & Hnik, 1971). In this model, an increase in the weight of a muscle is induced by functionally eliminating its synergist(s) (Binkhorst, 1969; Binkhorst & van't Hof, 1973;Goldberg, 1967; Goldberg et al, 1975; Gutmann & Hajek, 1971; Gutmann et al, 1969, 1970, 1971; Ianuzzo & Chen, 1978; Lesch et al, 1968; Mackova & Hnik, 1971, 1973; Reitsma, 1969; Rowe, 1969; Rowe and Goldspink, 1968; Seiden, 1976; Van Linge, 1962). The increase in weight has been associated with an increase in tetanic tension (Binkhorst, 1969; Binkhorst & van't Hof, 1973; Rowe, 1969; Van Linge, 1962), a decrease in tetanic tension (Gutmann et al, 1969), an increase in contraction time (Gutmann et al, 1969, 1970, 1971; Gutmann & Hajek, 1971) and no change in contraction time (Binkhorst, 1969; Binkhorst and van't Hof, 1973).

The increased muscle weight, tetanic tension and contraction time reported several times using the "compensatory hypertrophy" (CH) model are also found after strength training; however, reservations have been expressed about the suitability of the CH model as a model for "excessive use" or training (Edgerton et al, 1972; Gonyea & Ericson, 1976; Gutmann et al, 1971). A principal reservation has arisen from the observation that CH can be induced in a denervated muscle (Gutmann et al, 1969; Schiaffino & Hanzlikova, 1970; Sola et al, 1973). These and other experiments have led to the conclusion that CH is largely the result of passive tension developed within the muscle from being stretched by antagonists (Gutmann et al, 1969, 1971; Mackova & Hnik, 1970, 1971, 1973).

In contrast, the increased muscle size resulting from strength training is probably related to the high level of actively developed tension within the muscle during strength exercise. Thus, in endurance training, in which relatively weak contractions are repeated many times, there is little or no increase in muscle size.

In summary, both active (as in strength training) and passive (as in CH) tension can cause an increase in muscle size, tetanic tension and contraction time. Under normal physiological conditions, active tension is probably the dominant factor (Goldberg et al, 1975).

3. Muscle Fibres

Hypertrophy

In Man. An increase in muscle fibre cross-sectional area (hypertrophy) has occurred in an arm muscle (long head of triceps, Mac Dougall et al, 1977a) but not in a leg muscle (vastus lateralis, Penman, 1970; Thorstensson et al, 1976b) as a result of strength training. In all three of these investigations, there was a significant increase in voluntary strength but an increase in limb girth occurred only in the "arm" study. "Sprint" training resulted in increased voluntary strength and thigh girth but no change in fibre area in vastus lateralis (Thorstensson et al, 1975). The apparent contradiction between increased thigh girth but no increase in muscle fibre size would be resolved if hypertrophy occurred in other thigh muscles; it is known that vastus lateralis is used less in running than in, for example, cycling (Gollnick et al, 1973a). The greater trainability of the arm muscles than the leg muscles has been discussed above in relation to changes in muscle size.

Strength training causes hypertrophy of both fast twitch (FT) and slow twitch (ST) muscle fibres (MacDougall et al, 1977a) although hypertrophy occurs to a greater extent in FT fibres (MacDougall et al, 1977a; Thorstensson et al, 1976b). In contrast, endurance training has been shown to cause hypertrophy of slow twitch fibres only (Gollnick et al, 1973a).

These results of strength training experiments suggest that strength exercise recruits both FT and ST motor units whereas endurance exercise recruits preferentially the slow twitch motor units. Support for the suggestion comes from muscle glycogen depletion studies in man (glycogen depletion of a muscle fibre indicates recruitment). Long distance running (Costill et al, 1973), cycling at workloads corresponding to a small percentage of maximal oxygen uptake (Gollnick et al, 1974b) and sustained isometric contractions at less than 20% of maximal voluntary contraction (MVC) (Gollnick et al, 1974a) cause glycogen depletion primarily from ST fibres. In contrast, cycling at work loads corresponding to a high percentage (100% or more) of maximal aerobic power (Gollnick et al, 1973b, 1974b) and performing maximal isokinetic concentric contractions (Thorstensson & Karlsson, 1976) cause glycogen depletion from both FT and ST fibres. In sustained isometric contractions at greater than 20% MVC, FT fibres are depleted of glycogen (Gollnick et al, 1974a).

Also supportive are the results of electromyographic experiments in man. Low threshold motor units active during muscle contractions of low force (as in endurance training) are characterized by their small size, as indicated by motor unit potential amplitude (Gydikov and Kasarov, 1974; Person and Kudina, 1972; Stephens and Usherwood, 1975) and twitch tension (Milner-Brown et al, 1973). These small low threshold motor units possess a low maximal firing rate (Hannerz, 1974), a continuous firing pattern (Grimby and Hannerz, 1977; Hannerz, 1974; Warmolts & Engel, 1972), a high resistance to fatigue (Grimby & Hannerz, 1977; Gydikov & Kasarov, 1974; Hannerz, 1974; Stephens & Usherwood, 1975) and a long twitch contraction time (Milner-Brown et al, 1973). These studies suggest that the low threshold motor units are slow twitch motor units; further, Warmolts & Engel (1972) by combining electromyography and histochemistry with an open biopsy method, demonstrated that the muscle fibres of low threshold, continuous firing, fatigue resistant motor units possessed the histochemical properties of slow twitch fibres. In contrast, the high threshold motor units recruited only during maximal or near maximal contractions (as in strength training) are larger, have a higher maximal firing rate, fire intermittently, are less fatigue resistant, have a shorter twitch contraction time and possess the histochemical properties of FT fibres (for references, see corresponding characteristics of low threshold motor units).

The reason for the greater hypertrophy of FT relative to ST fibres after strength training is not known. Presumably, slow twitch motor units are contracting maximally during strength exercise (see above). Perhaps the FT fibres have greater potential for increasing size or are less "trained" prior to strength training. In this regard

Ashworth et al (1967) suggested that (strength) training is concerned with the high threshold motor units and referred to the popular use of heavy weights in training in order to exercise these otherwise inactive motor units.

In Animals. Weight lifting exercise has caused an increase in muscle fibre size (diameter or cross-sectional area) in the mouse (Goldspink, 1964), hamster (Goldspink & Howells, 1974), rat (Gordon et al, 1967b), Lesser Bushbaby (Edgerton, 1976) and cat (Gonyea & Ericson, 1976). The increased muscle fibre size has been associated with an increase (Edgerton, 1976; Gonyea & Ericson, 1976) and no change (Goldspink, 1964; Gordon et al, 1967b) in muscle weight. When the training has not produced an increase in muscle weight, it has been suggested that the training has not been of sufficient intensity or duration (Gonyea & Ericson, 1976).

In a non-human primate (Lesser Bushbaby), it was shown that weight training caused hypertrophy of fast twitch glycolytic (FG), fast twitch oxidative glycolytic (FOG) and slow twitch oxidative (SO) muscle fibres (for a discussion of muscle fibre typing, see Burke & Edgerton, 1975 and McComas, 1977, pp. 57-62), but the hypertrophy was greater in FG and FOG fibres; endurance training caused greater hypertrophy of FOG and SO fibres (Edgerton, 1976). Gonyea et al (1976) found that weight training in the cat caused hypertrophy of all fibre types although hypertrophy was greatest in the FG and FOG fibres. These authors also suggested that in studies where training had caused hypertrophy of only the initially small muscle fibres (Goldspink, 1964; Goldspink & Howells, 1974), the training had not been intense enough. Gordon et al (1967b) observed that weight lifting exercise caused greatest hypertrophy in fast twitch fibres, while endurance exercise (running and swimming) caused hypertrophy of both slow twitch and fast twitch fibres in the rat.

In summary, the effect of strength training upon muscle fibre size is similar in animals and man (see above); namely, strength training causes hypertrophy of all fibre types but the effect is greatest upon fast twitch (FG, FOG) muscle fibres. Endurance training has a relatively greater effect upon SO and FOG muscle fibres. The results of training in both man and animals suggest that in strength exercise all fibre types are recruited, while in endurance exercise SO and FOG fibres are selectively recruited. Supportive evidence for this suggestion in man has been discussed above. In animals, evidence in favour of this suggestion has been reviewed by Henneman & Olson (1965) and Burke & Edgerton (1975).

Functional elimination of synergists (compensatory hypertrophy model, CH) has resulted in an increase in muscle fibre size and in muscle weight in the overloaded muscles of the rat (Goldberg, 1965; Gutmann <u>et al</u>, 1971; Seiden, 1976) and mouse (Rowe, 1969). When CH was combined with running exercise, similar results were obtained (Reitsma, 1969; Van Linge, 1962). Gutmann <u>et al</u> (1971) observed hypertrophy of both FT and ST fibres in rat soleus in CH. Thus, the results obtained with CH were similar to those obtained with strength training in respect to muscle fibre size.

Fibre Number

<u>In Man</u>. There have been no reports of an increase in muscle fibre number within a muscle in man following strength training.

However, muscle fibre splitting has been observed in muscular dystrophy (Erb, 1891, cited by McComas, 1977) and in the hypertrophied rectus abdominis of a pregnant woman (Durante, 1902, cited by Reitsma, 1969).

Recent unpublished observations in body builders (Elder, G., MacDougall, J. D. and Sale, D. G.) are of interest, for they showed that while the body builders possess greatly enlarged triceps brachii muscles, analysis of muscle biopsy samples indicated that muscle fibre area was not significantly greater than in young men who had weight trained for a short period of time and in whom the triceps muscles had not become greatly enlarged. Thus, muscle fibre area could not account wholly for the massive triceps muscles of the body builders. One possible interpretation of the results is that prolonged, intense training induced an increase in fibre number as well as size; these changes have been demonstrated recently in an animal (see below). Another interpretation is that the body builders were born with a greater than average number of muscle fibres.

In Animals. An increase in muscle fibre number and fibre splitting without degenerative changes has been demonstrated in muscles of the cat after weight training (Gonyea et al, 1976). Goldspink & Howells (1974) did not find fibre splitting following weight lifting exercise in the hamster.

Fibre splitting has been induced using the CH model in the rat (Hall-Craggs, 1970) and mouse (Rowe & Goldspink, 1968). A combination of functional elimination of synergists and running has also induced fibre splitting in the rat (Reitsma, 1969; Van Linge, 1962).. When the CH model has been used, fibre splitting has often been associated with instances of fibre degeneration (Hall-Craggs, 1970; Reitsma, 1969; Van Linge, 1962) and it has been suggested that fibre splitting is a response to injury (Hall-Craggs, 1970). However, as noted above, strength training has induced fibre splitting without evidence of degeneration (Gonyea et al, 1976). This latter finding suggests that fibre splitting may be a normal adaptive response to functional overload in the form of strength training.

Sola et al (1973) obtained both hypertrophy and hyperplasia (increased fibre number) of muscle fibres in the anterior latissimus dorsi muscle of the chicken in response to stretch of the muscle (weights were attached to the wing). The amount of hypertrophy and hyperplasia was proportional to the degree of stretch. Of particular interest was the finding that the response occurred in both innervated and denervated muscle.

Fibre Type Distribution

In Man. Studies of endurance training (Gollnick et al, 1973a), "sprint" training (Thorstensson et al, 1975) and strength training (MacDougall et al, 1977a; Thorstensson et al, 1976b) have failed to show changes in the percentages of FT and ST muscle fibres within the trained muscles. However, a conversion of FG to FOG fibres has been demonstrated following endurance training (Andersen & Henriksson, 1977).

In Animals. Strength training (weight lifting) has caused an increase in the percentage of FG fibres and no change in the percentage of SO fibres in the palmaris longus of the cat (Gonyea & Bonde-Petersen, 1978); there were no changes in the flexor carpi radialis of the cat (Gonyea et al, 1976). Endurance training has caused an increase in the percentage of FOG fibres and no change in the percentage of SO fibres in the Lesser Bushbaby (Edgerton et al, 1972) and the gunea pig (Barnard et al, 1971; Peter et al, 1972). The unchanged percentage of SO fibres after endurance training was associated with no change in muscle twitch contraction time (Barnard et al, 1971; Edgerton et al, 1972; Peter et al, 1972) while the unchanged percentage of SO fibres following strength training was associated with an increase in contraction time (Gonyea & Bonde-Petersen, 1978; Gonyea et al, 1976). Thus, in these experiments, there is an apparent lack of correlation between changes in fibre type distribution and contraction speed.

In contrast to the effect of strength training, functional elimination of synergists (CH) resulted in an increase in the percentage of SO fibres within the affected muscle (rat plantaris, Ianuzzo & Chen, 1978); however, a similar experiment performed on a muscle already predominately slow in nature (rat soleus) resulted in no change in the percentage of a SO fibres (Gutmann et al, 1971). Employing a different model (immobilizing one hind limb), the consequent overloading of the contralateral limb resulted in an increase in the percentage of type I (SO) fibres within rat soleus (Eisen et al, 1973). Thus, the effect of muscle overloading upon fibre type distribution may depend upon the nature, degree and duration of the overload and upon the initial fibre type distribution of the muscle.

In summary, the results of training studies in both man and animals suggest that neither endurance nor strength training cause a change in the percentage of SO fibres within the trained muscle; however, endurance and strength training may result in an increase and decrease respectively in the percentage of FOG fibres.

4. Myofibrils and Myofilaments

In Man

Strength training has resulted in an increase in the cross-sectional area of myofibrils in brachial triceps; further, an increase in the number of myofibrils in the process of splitting was observed. There was no change in the volume density of the myofibrils within the muscle fibre. There was no change in the packing density of myofilaments within the myofibrils; therefore, the increased myofibril number and size was associated with an increase in the total number of myofilaments (MacDougall et al, 1976, 1978).

In Animals

Weight lifting exercise resulted in an increase in the number of myofibrils in mouse biceps muscle (Goldspink, 1964). Myofibrils increased to a certain size and then split (Goldspink, 1970). Functional elimination of synergists also caused an increase in the number and size of myofibrils in mouse soleus muscle (Rowe, 1969). However, endurance training (running) failed to cause an increase in the number of myofibrils in rat muscle although there was a trend toward more myofibrils at the ends of the muscle (Holmes & Rasch, 1958).

The increased number and size of myofibrils and thus the increased number of myofilaments would account for the increased contractile force of strength-trained muscle.

5. Biochemistry

Protein Synthesis and Degradation

In Animals. The increased muscle mass and associated increased muscle fibre size and number, increased myofibril size and number and increased number of myofilaments following strength training indicates that training causes an increase in the protein content of the trained muscle. The increased protein content could be the result of increased protein synthesis and/or decreased protein degradation within the muscle. The effects of increased muscle function upon protein synthesis and degradation has been recently reviewed by Goldberg et al (1975).

Employing the compensatory hypertrophy model in rat muscle, muscle growth has been associated with increased amino acid transport, increased protein synthesis and decreased protein degradation. It has also been demonstrated that the muscle growth is associated with increased DNA and RNA synthesis. In contrast to developmental muscle growth, this "work" hypertrophy can occur in the absence of growth hormone and insulin and during starvation. Tension developed within the muscle stimulates increased amino acid transport, for when both hemidiaphragms of the rat were stimulated, such that one contracted isometrically and one shortened against no load, amino acid transport was greater in the former. Passive stretch of a muscle will also increase protein synthesis and decrease protein degradation (Goldberg _et al_, 1975).

Myofibrillar vs. Sarcoplasmic Protein

In Animals. Endurance training has been found to increase the concentration of sarcoplasmic protein (i.e. all protein exclusive of myofibrillar and stromal protein) within the trained muscle while strength training increased the concentration of myofibrillar protein (Gordon _et al_, 1967a, b; Jaweed, _et al_, 1974). These findings are in agreement with an hypothesis recently proposed by Edgerton (1976) that endurance training leads to an increase in metabolic protein within the muscle while strength training leads to an increase in contractile protein.

Seiden (1976) observed a decrease in myofibrillar volume density and an increase in mitochondrial volume density in compensatory hypertrophy, while swimming exercise resulted in no change in these two measures. Helander (1961) found an increase in myofibrillar protein concentration after running exercise and an increase in sarcoplasmic protein concentration after inactivity.

In Man. Strength training has resulted in a decrease in the mitochondrial volume density of triceps brachii (MacDougall et al, 1978).

Thus, the results of experiments in animals and man suggest a specificity of training response; namely, strength training causes an increase in myofibrillar protein concentration and thus increased contractile force, while endurance training causes an increase in sarcoplasmic protein and thus increased endurance. Some of the observed changes in protein concentration may have been related to changes in fibre type distribution within the trained muscles (as discussed above). The apparent dilution of sarcoplasmic protein in strength-trained muscle could conceivably result in reduced endurance.

Energy Metabolism (Substrate)

In Man. Strength training has been associated with increased resting levels of adenosine triphosphate (ATP), creatine phosphate (CP and glycogen in the trained brachial triceps muscle (MacDougall et al, 1977b). These substrates would be repeatedly used during strength exercise (MacDougall et al, 1977b; Thorstensson et al, 1976b). However, strength training (isometric training, Grimby et al, 1973) failed to change resting levels of ATP, CP and glycogen in vastus lateralis and sprint training of this same muscle failed to change resting concentrations of ATP and CP (Thorstensson et al, 1975). The absence of changes in the latter studies may be related to the lesser trainability of the leg muscles in comparison to the arm muscle (see discussion of muscle size above). Endurance training has also been associated with increased concentrations of glycogen (Gollnick et al, 1973a), ATP (Eriksson et al, 1973; Karlsson et al, 1971, 1972) and CP (Eriksson et al, 1973).

It is difficult to relate the increased storage of substrate to the increased contractile force which results from strength training; however, increased storage of CP and ATP would allow high levels of force to be maintained for longer periods, as suggested by MacDougall et al (1977b).

Energy Metabolism (enzymes)

In Man. Strength training (weight lifting) has resulted in an increased activity level of one enzyme (myokinase) involved in anaerobic metabolism but in no change in activity level in other enzymes (magnesium stimulated ATPase; creatine phosphokinase, CPK; and phosphofructokinase, PFK) in vastus lateralis (Thorstensson et al, 1976b). In this same muscle, sprint training (5s treadmill runs at high velocity and steep inclination) resulted in increased activity of myokinase, magnesium stimulated ATPase and CPK but no change in lactate dehydrogenase (LDH). It was suggested that a biological implication of the increased enzyme activities would be to enhance ATP resynthesis for extreme muscle activities, such as sprinting (Thorstensson et al, 1975). However, isometric strength training (a series of brief maximal contractions) has also resulted in an increased activity level of an oxidative enzyme, succinic oxidase (Grimby et al, 1973). Endurance training (cycling for one hour at a workload corresponding to 75% of maximal aerobic power) has been shown to increase the activity level of enzymes involved in both aerobic and anaerobic metabolism (Gollnick et al, 1973a).

In Animals. Weight lifting training in the rat has resulted in increased activity of succinic acid dehydrogenase and phosphorylase (Kowalski et al, 1969) while isometric training has resulted in increased activity of creatine kinase and citrate synthetase (Exner et al, 1973a, b) of the trained muscles. Sprint training in the rat resulted in increased activity levels of hexokinase, citrate synthetase, glycogen phosphorylase, triose phosphate dehydrogenase and creatine kinase in the trained muscles (Staudte et al, 1973). Thus, high intensity training affects the activity level of enzymes involved in both aerobic and anaerobic metabolism.

Nervous System

Research in Man

It has often been suggested that the increased voluntary strength that occurs in man following strength training is in part a learned act, implying that adaptation has occurred within the nervous system (Bonde-Petersen, 1960; Darcus, 1956; Darcus & Salter, 1955; Delorme *et al*, 1950; Rose *et al*, 1957; Ward & Fisk, 1964). It has been postulated that the trained individual has learned to activate more motor units (Darcus, 1956; Lundervold, 1951; Thorstensson *et al*, 1976b) and to eliminate unnecessary muscle activity (Lundervold, 1951). Several kinds of experimental evidence support the hypothesis that adaptation occurs within the nervous system during strength training. The evidence is enumerated below.

1. Rapid Initial Increases in Strength

The initial increases in strength in a training programme are very rapid and it is unlikely that muscle hypertrophy could account for these initial increases (Hellebrandt & Houtz, 1956). In fact, improvement in strength has been demonstrated within the first training session (Whitley & Elliott, 1968).

2. Increased Strength Without Hypertrophy

Increased voluntary strength has occurred after training without an increase in gross muscle size (Liberson & Asa, 1959; Penman, 1970; Rose *et al*, 1957; Tanner, 1952; Thorstensson *et al*, 1976b; Ward & Fisk, 1964) or muscle fibre size (Penman, 1970; Thorstensson *et al*, 1976b). One possible interpretation of these findings is that adaptation within the nervous system accounted for a large portion of the increased strength.

3. Specificity of Training

When the same apparatus is used for both training and testing, the measured increases in strength are greater than when different apparatus is used for training and testing (Bonde-Petersen, 1960; Leister, 1965). Thorstensson et al (1976b) observed that eight weeks of weight training increased weight lifting strength by 67% but strength measured on an isometric dynamometer increased by only 13%. Hellebrandt et al (1947) found that an isometric strength test failed to indicate an increase in strength although weight lifting strength greatly improved after weight training. Following weight training programmes, voluntary strength measured by weight lifting increased significantly, while strength measured on an isokinetic dynamometer did not increase (Fahey & Brown, 1973; Pipes & Wilmore, 1975). If increased voluntary strength with training were only the result of changes within the muscles, various methods of measuring strength should give similar results. That this is not the case suggests that the nervous system is involved in the training response.

4. Cross-training

Training of one limb is associated with significant increases in strength of the contralateral untrained limb (Coleman, 1969; Darcus & Salter, 1955; Hellebrandt et al, 1947; Mathews et al, 1956; Rasch & Morehouse, 1957; Slater-Hammel, 1950; Wagnar, 1970). The effects of skill training can also be transferred in this manner (Hellebrandt, 1951). These findings suggest that adaptation within the nervous system occurs during training. It has been demonstrated that unilateral strength exercise evokes motor unit activity in the contralateral limb (Gregg et al, 1957; Moore, 1975; Sills & Olson, 1958; Stish, 1958); however, the amount of recorded activity (EMG) was not large and it is probable that little adaptation would occur within the muscle in this situation.

5. Unilateral vs. Bilateral Strength Performance

Untrained subjects performing a bilateral leg strength test are not capable of matching the sum of the forces produced by the legs performing singly, and it has been suggested that fibre recruitment is restricted in bilateral compared to unilateral leg exercise (Secher et al, 1977). Further, trained individuals are able, in their bilateral performance, to match the sum of separate left and right unilateral performances. (Secher, 1975; Tesch & Karlsson, 1978). It has been suggested that with training there is an increased ability to recruit motor units during bilateral leg exercise (Tesch & Karlsson, 1978).

6. Disinhibition

According to Darcus (1956), the improvement in muscle strength by training may also be due to a reduction in inhibitory impulses originating in the periphery (Golgi tendon organ) or passing down from higher centres. Studies of the reticular system suggest that the effect of training may be a reduction of the inhibiting effect of the extrapyramidal system on the motoneurons (Magoun, 1959). Morehouse (1960) and Morehouse & Miller (1976, p. 56) have also favoured the disinhibition theory of strength development. Related to this theory is the finding that strength performance is increased under hypnosis (Ikai & Steinhaus, 1961; Roush, 1951) except in individuals who are already highly trained (Ikai & Steinhaus, 1961). In addition, auditory stimuli (shouting, gunshots) just prior to strength trials increase performance (Ikai & Steinhaus, 1961). These findings suggest that under normal conditions most individuals are incapable of activating all motor units; however, in unusual circumstances or with training, individuals can activate more motor units, presumably as a result of disinhibition. Also relevant is the recent finding that in patients who had undergone partial amputation of one arm, inhibition was significantly diminished in the other arm (triceps), possibly as a result of overuse (McComas et al, 1978).

7. Motor Unit Synchronization

While the evidence discussed above supports the hypothesis that the response to strength training involves the nervous system, it does not include an actual measurement of adaptive change within the nervous system. In this and the following sections the results of quantitative measurements of neural function before and after strength training are presented.

Synchronization of motor units became more pronounced in a group of subjects after a six week strength training programme. Further, motor unit synchronization was enhanced in weight lifters and in subjects involved in manual jobs which required large, brief forces to be exerted (Milner-Brown et al, 1975). On the basis of the results of reflex experiments (see below), these authors postulated that the increased motor unit synchronization was caused by enhanced descending inputs to motoneurons from supraspinal centres.

8. Reflex Potentiation

Upton et al (1971) developed a method for measuring the degree to which motoneuron excitability is raised during maximal voluntary muscle contractions. The method, which involves electromyography and percutaneous nerve stimulation, consists of measuring the extent to which voluntary contraction potentiates recorded reflex responses. There is a positive correlation between the degree of voluntary effort and the degree of reflex potentiation.

The method was employed in a study of elite sprinters (runners) and it was found that the sprinters possessed a greater level of reflex potentiation than a group of normal control subjects (Upton & Radford, 1975). Reflex potentiation has also been found to be enhanced in weight lifters (Milner-Brown et al, 1975). One of these weight lifters was investigated after a two month lay-off from training; reflex potentiation declined, suggesting that the previous higher level was due in part to training and not all due to genetic endowment (however, a six week strength training programme with four subjects failed to cause a significant change in reflex potentiation). These investigators also observed that the enhancement was greater for the longer compared to the shorter latency reflexes. The decline with inactivity was also greater for the longer latency reflexes. These findings were interpreted as suggesting that adaptive changes occurred in supraspinal pathways.

9. Motor Nerve Conduction Velocity

Burke (1971) found that 12 weeks of isometric strength training had no effect upon ulnar motor nerve conduction velocity.

10. Reflex Time and Reaction Time

Strength training has resulted in a significant decrease in patellar (Francis & Tipton, 1969) and triceps surae (Reid, 1967) reflex time. In the latter investigation, the decrease in monosynaptic reflex time was interpreted as indicating an increase in nerve conduction velocity.

Strength training has also resulted in significant decreases in reaction time (Bates, 1967; Crowder, 1966; Michael, 1963; Parker, 1960). Possible mechanisms underlying this finding would include increased nerve conduction velocity and/or faster integration within the central nervous system.

Research In Animals

There have been no studies in animals of the effects of strength training upon the nervous system; however, the effects of endurance training have been investigated. In addition, other models of hyperactivity have been employed to study adaptive changes within the nervous system. Some of these investigations are reviewed below.

1. Nerve Fibre Diameter and Conduction Velocity

Endurance exercise (running, swimming) in rodents has resulted in an increase (Sammeck, 1975; Samorajski & Rolsten, 1975), a decrease (Andersson & Edstrom, 1957) and no change (Tomanek & Tipton, 1967) in nerve fibre diameter. The variation in the findings of these studies could be related to the variation in the intensity and duration of training, as suggested by Samorajski & Rolsten (1975).

Partial deneuritization (Edds, 1949), denervation of synergists (Edds, 1950) and immobilization of one hind limb (Eisen <u>et al</u>, 1973) have all resulted in increased diameter of nerve fibres innervating the overloaded muscles.

Sammeck (1975) observed that the increased nerve fibre diameter following swimming training in the rat was associated with increased myelin thickness (more spiral turns of sheath). In view of the demonstrated positive correlation between conduction velocity and nerve fibre diameter (Hursh, 1939) and myelin sheath thickness (Sanders & Whitteridge, 1946), it is tempting to speculate that an increase in nerve conduction velocity occurred in those studies where an increase in nerve fibre diameter and myelin sheath thickness were found. In fact, an increase in nerve conduction velocity in the peripheral nerves of the rat after endurance training has been reported (Retzlaff & Fontaine, 1965).

Edds (1950) had suggested that the increased nerve fibre diameter was due to increased metabolic rate in the soma of the neuron and a consequent increased rate of axoplasmic flow. According to Samorajski & Rolsten (1975), it is still uncertain whether nerve fibre diameter changes result from increased neural activity <u>per se</u> or from changes in muscle mass.

2. Synaptic Transmission.

Eccles (1953, 1958) hypothesized that use leads to an increase and disuse leads to a decrease in the synaptic potency. The hypothesis is supported by the evidence that monosynaptic reflex amplitude was increased after denervation of synergists (Eccles <u>et al</u>, 1959, 1962).

Further, monosynaptic reflex activity was enhanced in segments of spinal cord adjacent to those affected by dorsal root section (Eccles & McIntyre, 1953). According to Kandell & Spencer (1968), however, these experiments failed to determine whether the observed changes were due to increased usage or pathological manifestations of the surgical procedures employed. These authors also cited the review by Sharpless (1964), who presented evidence for the contrary view that decreased synaptic usage can lead to a compensatory increase in synaptic potency.

Given the assumption that increased usage enhances synaptic function within the central nervous system, Morrell (1961) reviewed the possible anatomical correlates which include swelling of afferent terminals (Eccles & McIntyre, 1953) and multiplication and branching of axon terminals (Hebb, 1949; Konorski, 1950). Kandell & Spencer (1968) cited the hypothesis of Hyden (1965) who held that a particular pattern of impulse activity caused de-repression of DNA, which led to a new messenger RNA which led to new protein formation (enzyme), which led to a new end-product (transmitter) which resulted in increased synaptic efficacy.

Hyperactivity has been reported to affect enzyme activity at the neuromuscular junction. Endurance training in the rat caused an increase in the activity of endplate and non-endplate cholinesterase in white vastus lateralis but not in soleus or red vastus lateralis. There was no effect upon choline acetyltransferase (Crockett _et al_, 1976). The overloading of rat plantaris muscle by functional elimination of synergists resulted in increased activity of both choline acetyltransferase and acetylcholinesterase (Snyder _et al_, 1973). The physiological significance of these changes is not clear; however, they may mediate an adaptation consisting of increased synthesis and inactivation of acetylcholine in response to increased endplate activity (transmitter release).

3. Changes Within the Nerve Cell Soma

Gilliam et al (1977) reported that sprint training as opposed to endurance training had a retarding effect on the growth of soma size in the rat. Following endurance training (swimming) in the guinea pig, Edstrom (1957) found no change in the size of soma or nucleus; however, the size of the nucleolus was significantly increased, a sign of intensified protein synthesis. Edgerton (1976) reviewed the effects of exercise upon the soma and referred to the work of Dolley (1909) and Gerchman et al (1975) which demonstrated changes (e.g. enhanced acid phosphatase activity) related to protein synthesis; however, as pointed out by Edgerton (1976), these findings are difficult to relate to endurance or strength performance.

Effects of Immobilization

Voluntary Strength

In Man

Joint immobilization in human limbs results in a decrease in voluntary strength. Dietrick et al (1948) observed isometric strength decreases of 13% and 21% in dorsi flexion and plantar flexion respectively after 6.5 weeks of immobilization in leg casts in four young men. In one subject, Hills & Byrd (1973) found a 44% decrease in handgrip strength after four weeks of immobilization in a forearm cast. Stillwell et al (1967) applied casts to one leg of 22 young adults for two weeks. Knee extension strength decreased by approximately 30%. Muller (1970) reviewed studies on cast immobilization; two weeks of immobilization resulted in an average decrease in strength of 25-30%.

The decrease in voluntary strength after immobilization can be attributed to relative "disuse" of the involved muscles, for when subjects were instructed to perform isometric contractions regularly while the limb was immobilized, a loss in strength was prevented (Stillwell et al, 1967). In animal research, immobilization in the Lesser Bushbaby (Edgerton et al, 1975a) and in the rat (Fischbach & Robbins, 1969) was associated with markedly reduced but not abolished motor unit activity in the immobilized muscles. Therefore, immobilization is an effective method for inducing relative inactivity in muscle groups.

In Animals

To the author's knowledge, there have been no studies on the effects of immobilization upon voluntary strength in animals, probably because of methodological difficulties related to strength measurement.

Muscle

1. Contractile Properties

In Man

To the author's knowledge, there have been no studies in man on the effects of immobilization upon the contractile properties of muscle contractions evoked by indirect nerve stimulation.

In Animals

(1) Twitch and Tetanic Tension. In contrast to strength training, immobilization results in a decrease in isometric twitch tension. A decrease in twitch tension has been found in the gastrocnemius of the guinea pig (Maier et al, 1976), the soleus, gastrocnemius and flexor digitorum longus of the cat (Cooper, 1972) and the soleus and

tibialis anterior of the kitten (Mann & Salafsky, 1970) after immobilization. However, no significant change in twitch tension was observed in the plantaris of the Lesser Bushbaby (Edgerton et al, 1975a) or guinea pig soleus (Maier et al, 1976) after immobilization.

Similarly, there is a decrease in tetanic tension following immobilization. This has been observed in cat soleus, gastrocnemius, and flexor digitorum longus (Cooper, 1972), kitten soleus (Mann & Salafsky, 1970), rat soleus (Fischbach & Robbins, 1969; Wells, 1969) and guinea pig gastrocnemius (Maier et al, 1976). However, no significant change was found in the plantaris of the Lesser Bushbaby (Edgerton et al, 1975a), guinea pig soleus (Maier et al, 1976) or kitten tibialis anterior (Mann & Salafsky, 1970).

When twitch and tetanic tension are expressed per unit muscle mass rather than absolutely, immobilization results in an increase in twitch and tetanic tension in fast muscles such as guinea pig gastrocnemius (Maier et al, 1976), plantaris of the Lesser Bushbaby (Edgerton et al, 1975a) and rabbit gastrocnemius (Fischer & Ramsey, 1946). In addition, Maier et al (1976) pointed out that the data of Mann & Salafsky (1970) indicated a similar result, for a non-significant increase in tetanic tension of kitten tibialis anterior after immobilization was coupled with a significant decrease in muscle weight. Related to these findings was the observation by Burke et al (1975) that fibre diameter was proportionately more reduced than maximum tetanic tension in single FG motor units of immobilized cat gastrocnemius. In contrast an increase in tension per unit muscle mass (specific tension) was not found in slow guinea pig (Maier et al, 1976) or kitten (Mann & Salafsky, 1970) soleus after immobilization. In explaining the difference in response between fast and slow muscles, Maier et al (1976) referred to the work of Tomanek & Lund (1974) which showed greater deterioration of the contractile apparatus in the immobilized soleus as opposed to fast-twitch muscle. The mechanism for the increased specific tension of fast-twitch muscle after immobilization is unknown (for a review of possible mechanisms, see Maier et al, 1976).

(2) Contraction Time and Half Relaxation Time. Immobilization of the slow soleus muscle in the guinea pig (Maier et al, 1976), rat (Booth & Kelso, 1973a; Fischbach & Robbins, 1969) and kitten (Mann & Salafsky, 1970) resulted in a decrease in twitch contraction time. Cooper (1972) observed an increase in contraction time in immobilized cat soleus. No significant change in contraction time occurred after immobilization in fast plantaris of the Lesser Bushbaby (Edgerton et al, 1975a), guinea pig gastrocnemius (Maier et al, 1976) rat rectus femoris (Booth & Kelso, 1973a) and kitten tibialis anterior (Mann & Salafsky, 1970). Cooper (1972) observed an increase in contraction time in immobilized cat gastrocnemius and flexor digitorum longus.

Half relaxation time has been reported to decrease in immobilized guinea pig soleus (Maier et al, 1976) but to increase in immobilized cat soleus (Cooper, 1972). Half relaxation time did not change significantly after immobilization in the plantaris of the Lesser Bushbaby (Edgerton et al, 1975a) and guinea pig gastrocnemius (Maier et al, 1976); however an increase in half relaxation time was reported in immobilized cat gastrocnemius and flexor digitorum longus (Cooper, 1972).

Therefore, the general finding (with the exception of the findings of Cooper, 1972), has been for immobilization to cause a "speeding up" of slow muscle and to leave fast muscle unchanged in contraction and half relaxation time. The mechanisms responsible for the changes in contractile speed are not known (see however, the discussion of the effect of immobilization upon fibre type conversion below); this subject has been recently discussed by Maier et al (1976).

It should be recalled that this general finding in relation to immobilization is in contrast to the general finding in relation to strength training (a "slowing" of muscle contraction).

2. Muscle Size

In Man

Immobilization has resulted in a decrease in muscle size as measured by limb girth (Deitrick et al, 1948; Ingemann-Hansen & Halkjaer-Kristensen, 1977; MacDougall et al, 1977b) and limb volume (Ingemann-Hansen & Halkjaer-Kristensen, 1977; Sargeant et al, 1977). Ingemann-Hansen & Halkjaer-Kristensen (1977) found that 30 days of thigh immobilization resulted in a 6% decrease in thigh circumference, an increase in subcutaneous fat thickness, a 17% decrease in lean thigh volume and no change in fat volume; they concluded that the loss of thigh volume due to loss of muscle was partly concealed by an unchanged fat volume.

In Animals

In animals, changes in muscle size as a result of immobilization have usually been measured as changes in muscle weight. Thus, immobilization has resulted in a decrease in muscle weight in rat soleus (Eccles, 1944; Goldspink, 1977; Herbison et al, 1978), extensor digitorum longus

(Goldspink, 1977) and in gastrocnemius and plantaris (Herbison *et al*, 1978); in cat soleus (Cooper, 1972; Mann & Salafsky, 1970), tibialis anterior (Mann & Salafsky, 1970) and gastrocnemius and flexor digitorum longus (Cooper, 1972); in rabbit gastrocnemius (Ferguson *et al*, 1957; Fischer & Ramsey, 1946) and tibialis anterior (Ferguson et al, 1957); in guinea pig soleus and gastrocnemius (Maier *et al*, 1976); in monkey gastrocnemius and soleus (Chor & Dolkart, 1936); and in plantaris, soleus, gastrocnemius, tibialis anterior, vastus lateralis, vastus medialis and vastus intermedius of the Lesser Bushbaby (Edgerton *et al*, 1975a).

Some muscles decrease in muscle weight in response to immobilization to a greater extent than others. In particular, soleus atrophies more than other hind limb muscles (Eccles, 1944; Edgerton *et al*, 1975a; Mann & Salafsky, 1970; Summers & Hines, 1951; Thomson & Luco, 1944). However, Booth & Kelso (1973b), Cooper (1972) and Herbison *et al* (1978) found that atrophy of soleus was similar to that of other leg muscles (although Cooper, 1972, noted that atrophy of soleus was more rapid). Maier *et al* (1976) found a greater weight loss in gastrocnemius than soleus. Edgerton *et al* (1975a) observed the effect of immobilization upon ten hind limb muscles in the Lesser Bushbaby; the general finding was greater weight loss in extensor compared to flexor muscles, a result also found by Thompson (1934) and Wells (1969). Edgerton *et al* (1975a) suggested that this finding might be expected because the relative decrease in demands caused by immobilization would be greater in the antigravity extensors than the flexors. Edgerton *et al* (1975a) also discussed how different groups of muscles (e.g. calf vs. thigh muscles) could be affected differently by immobilization.

Another factor which affects the degree of muscle atrophy during immobilization is the length at which the muscle is immobilized. Muscle atrophy is greater when the muscle is immobilized in a shortened versus a lengthened position (Ferguson et al, 1957; Goldspink, 1977; Ralston et al, 1952; Summers & Hines, 1951; Thomsen & Luco, 1944). Further, a muscle immobilized in a lengthened position may increase in weight (Ferguson et al, 1957; Goldspink, 1977; Thomsen & Luco, 1944; the role of passive tension in muscle hypertrophy was discussed above in relation to the effects of training).

In summary, the general finding is that immobilization causes a decrease in muscle mass. This finding is in contrast to the effect of strength training, which causes an increase in muscle mass.

3. Muscle Fibres

Fibre Size (diameter, area)

In Man. Atrophy of muscle fibres has been reported in brachial triceps (MacDougall et al, 1977a) and vastus lateralis (Edstrom, 1970; Sargeant et al, 1977) following immobilization. In brachial triceps, greater atrophy occurred in FT (Type II) fibres while in vastus lateralis greater atrophy occurred in ST (Type I) fibres. This difference in the pattern of atrophy in vastus lateralis and triceps may be related to the normal use of these muscles. Thus, vastus lateralis is a postural muscle and ST fibres would be very active relative to FT fibres in normal activity. In contrast, triceps would be used intermittently and in "phasic" contractions involving FT fibres. Therefore, it is possible that within a muscle, those motor units which are normally heavily used are most susceptible to atrophy during immobilization (MacDougall et al, 1977a). A similar suggestion has been made in relation to the results of animal experiments (see below).

In Animals. Following immobilization, fibre atrophy has been shown in cat gastrocnemius (Burke et al, 1975; Cooper, 1972) and soleus and flexor digitorum longus (Cooper, 1972); in monkey gastrocnemius and soleus (Chor & Dolkart, 1936); in rat soleus (Fischbach & Robbins, 1969; Herbison et al, 1978) and plantaris and gastrocnemius (Herbison et al, 1978); in guinea pig gastrocnemius (Karpati & Engel, 1968; Maier et al, 1976), soleus (Maier et al, 1976; Tomanek & Lund, 1974) and vastus lateralis (Tomanek & Lund, 1974); and in the plantaris, soleus and vastus intermedius of the Lesser Bushbaby (Edgerton et al, 1975a).

There is evidence of preferential atrophy of specific fibre types following immobilization. Thus, greater atrophy of ST versus FT fibres occurred in rat soleus (Booth & Kelso, 1973a) and tibialis anterior (Jaffe et al, 1978); in cat gastrocnemius (Burke et al, 1975); in guinea pig gastrocnemius (Maier et al, 1976) and vastus lateralis (Tomanek & Lund, 1974); and in plantaris, vastus intermedius, vastus lateralis, tibialis anterior and gastrocnemius of the Lesser Bushbaby (Edgerton et al, 1975a). Greater atrophy of FOG versus FG fibres has been reported in rat tibialis anterior (Jaffe et al, 1978); in guinea pig gastrocnemius (Maier et al, 1976); and in plantaris, vastus lateralis and gastrocnemius of the Lesser Bushbaby (Edgerton et al, 1975a). Herbison et al (1978) found preferential atrophy of FT fibres in rat plantaris. Contrary to findings cited above, no preferential atrophy was found in rat soleus (Fischbach & Robbins, 1969; Herbison et al, 1978) or guinea pig gastrocnemius (Karpati & Engel, 1968).

As discussed in relation to human experiments above, preferential atrophy of fibre types within a muscle may be related to the normal use of the muscle prior to immobilization. For example, Herbison et al (1978) found similar atrophy of FT and ST fibres in rat soleus but greater atrophy of FT fibres in plantaris. These authors suggested that the normal activity of soleus involves both fibre types; but in plantaris, FT fibres are preferentially used. Consistent with their suggestion were the normal FT/ST fibre diameter ratios in the two muscles; the ratio was considerably higher in plantaris than in soleus.

In summary, immobilization results in muscle fibre atrophy, which is in contrast to the effect of strength training (hypertrophy). Immobilization apparently causes preferential atrophy of ST or FT muscle fibres depending upon the normal use of the muscles; strength training tended to cause greater hypertrophy of FT fibres.

Fibre Type Distribution

In Man. Immobilization of brachial triceps resulted in no change in fibre type distribution (% FT vs % ST, MacDougall et al, 1977a).

In Animals. A decrease in the percentage of ST fibres after immobilization has been found in rat soleus (Booth & Kelso, 1973a; Fischbach & Robbins, 1969; Herbison et al, 1978); in guinea pig soleus (Maier et al, 1976); and in soleus and vastus intermedius of the Lesser Bushbaby (Edgerton et al, 1975a). This change in fibre type distribution may be partly responsible for the decrease in contraction time of slow muscle following immobilization (for references, see above). In contrast, nominally fast muscles do not change in fibre type distribution after immobilization, as shown in rat rectus femoris (Booth & Kelso, 1973a) and plantaris (Herbison et al, 1978); in guinea pig gastrocnemius (Maier et al, 1976); and in several fast hind limb muscles of the Lesser Bushbaby (Edgerton et al, 1975a). These findings may be related to the fact that contraction time does not usually change in fast muscles after immobilization (for references, see above).

4. Myofibrils and Myofilaments

In Man

Immobilization caused in brachial triceps a decrease in myofibril size and number and a decreased incidence of splitting myofibrils. There was no change in myofilament packing density; thus, there was a decrease in the number of myofilaments within muscle fibres (MacDougall et al, 1976).

In Animals

Immobilization of skeletal muscles of the cat (Cooper, 1972) and guinea pig (Tomanek & Lund, 1974) resulted in a decrease in myofibril number and diameter and a consequent loss of myofilaments.

Thus, the findings in man and animals are similar and the decrease in contractile protein could account for the decrease in twitch and tetanic tension reviewed above and for the decrease in fibre and gross muscle size. In contrast, strength training, as reviewed above, has a reverse effect; namely, increased number of myofilaments and myofibrils, increased myofibril size, increased fibre and muscle size and increased contractile force.

5. Biochemistry

Protein Synthesis and Degradation

In Animals. In the rat, immobilization of hind limb muscles in a shortened position (but probably not in a lengthened position; see review of effect of immobilization upon muscle size above) resulted in a decrease in the rate of protein synthesis and an increase in the rate of protein degradation, the former being more prominent. These changes were associated with a decrease in DNA synthesis and RNA concentration (Goldspink, 1977). Thus, the effect of immobilization upon protein synthesis and degradation is the reverse of the effect of functional overload (for discussion see above).

The decreased protein synthesis and increased protein degradation in immobilized muscle would lead to a decrease in total protein content of the muscle.

Myofibrillar vs. Sarcoplasmic Protein

<u>In Animals</u>. A greater loss of myofibrillar compared to sarcoplasmic protein has been observed in skeletal muscle following immobilization (Fischer & Ramsey, 1946; Helander, 1957; Herbison <u>et al</u>, 1978). The data of Maier <u>et al</u> (1976) also indicates a trend toward greater loss of myofibrillar than sarcoplasmic protein. In contrast, strength training results in a proportionately greater increase in myofibrillar than sarcoplasmic protein (see above).

Energy Metabolism (Substrate)

<u>In Man</u>. Immobilization of brachial triceps resulted in a decrease in the resting concentrations of creatine phosphate (CP) and glycogen but no change in adenosine triphosphate (ATP), while strength training resulted in an increase in resting concentrations of CP, ATP, and glycogen (MacDougall <u>et al</u>, 1977b).

<u>In Animals</u>. Ferguson <u>et al</u> (1957) found a decrease in the concentration of glycogen and creatine in immobilized rabbit gastrocnemius.

Energy Metabolism (Enzymes)

In Animals. Long term immobilization of skeletal muscle did not result in significant changes in the activity of enzymes associated with anaerobic or aerobic metabolism (Edgerton et al, 1975a; Mann & Salafsky, 1970). Edgerton et al (1975a) interpreted their findings as indicating that when metabolic demands are suddenly and greatly reduced, adjustments are initiated immediately to accommodate the new level of muscular activity.

Nervous System

In Man

To the author's knowledge, there have been no studies on the effect of immobilization upon neural function in man.

In Animals

Nerve Fibre Diameter. Immobilization resulted in a decrease in nerve fibre diameter in the nerve supplying rat soleus (Eisen et al, 1973) but not in the nerve supplying medial gastrocnemius (Tomanek, 1968). In young rats, immobilization retarded myelination of nerve fibres (Tomanek, 1968). The difference in the response of the nerves to rat soleus and gastrocnemius may be related to the relatively greater effect of immobilization upon soleus than other muscles (see above).

In contrast, hyperactivity has resulted in an increase in nerve fibre diameter and a thickening of the myelin sheath (see above).

Neuromuscular Junction. The motor end plates of rat gastrocnemius have been reported to decrease in size in parallel with the decrease in muscle fibre size following immobilization (Cole, 1960). Fischbach &

Robbins (1971) found a small spread of extra junctional acetylcholine sensitivity following immobilization of rat soleus. Snyder et al (1973) observed a decrease in the activity of choline acetyl transferase and acetylcholine esterase at rat neuromuscular junction following immobilization.

Neuromuscular Function in Athletes

Voluntary Strength

The evidence indicating that strength training does increase voluntary strength has been reviewed above. It would be expected, therefore, that groups of athletes who employ strength training, or whose sports performance is a form of strength training, to have greater strength than untrained control subjects or endurance athletes. Thus, it has been demonstrated that weight-lifters possess greater isometric leg strength than untrained control subjects and endurance athletes (Edstrom & Ekblom, 1972; Tornvall, 1963). Sprinters, jumpers, throwers and downhill skiers possess greater isometric leg strength than untrained controls or endurance athletes such as cross country skiers, long distance runners and orienteers (Komi et al, 1977; Thorstensson et al, 1977).

One factor which affects the results obtained is the type of muscle contraction used in the testing and also the speed of contraction. When sprinters and jumpers perform knee extension at a joint angular velocity of 180 deg/s they are much stronger relative to other groups than when they perform isometric (0 deg/s) knee extension. In contrast, the performance of endurance athletes (orienteers, walkers) is relatively poorer at the higher velocity (Thorstenson et al, 1977).

The question arises as to what extent the superior strength performance of certain groups of athletes is due to training and due to genetic endowment. It has already been established that strength training increases voluntary strength; further, the data of Tornvall (1963) also suggest that training is an important factor. The strength performance of weight lifters relative to controls varied depending on the muscle group. Although the weight lifters exceeded the control subjects in all measures, the difference was greatest in those muscle groups directly involved in competitive weight lifting. Below, evidence is presented which suggests that genetic endowment is also important.

Muscle

Muscle Size

A positive correlation has been demonstrated between the cross sectional area of a muscle and its strength (Ikai & Fukunaga, 1968). Haggmark et al (1978), employing soft tissue X-rays, found that weight lifters possessed greater thigh cross sectional area and thigh muscle cross sectional area than controls and endurance athletes. The endurance athletes were similar to controls in these measurements. Thus, there is a correlation between the muscle size measurements in these groups and voluntary strength (see above) indicating that variation in muscle size is one factor accounting for the variation in voluntary strength found in groups of athletes.

Muscle Fibre Size

The FT fibre area of vastus lateralis has been reported to be greater in weight lifters than in controls or endurance athletes (Edstrom & Ekblom, 1972; Gollnick et al, 1972; Haggmark et al, 1978;

Prince et al, 1976). The ST fibre area is also enlarged in some (Gollnick et al, 1972; Haggmark et al, 1978; Prince et al, 1976) but not all (Edstrom & Ekblom, 1972) weight lifters. Thus, the ratio of FT to ST fibre area is greater in weight lifters than in controls and endurance athletes (Edstrom & Ekblom, 1972; Gollnick et al, 1972; Haggmark et al, 1978; Prince et al, 1976). These findings are in agreement with those of strength training studies (see above).

Sprinters and jumpers also tend to have a relatively high FT/ST fibre area ratio (Thorstennson et al, 1977).

Fibre Type Distribution

A positive correlation has been demonstrated between a high percentage of FT fibres within vastus lateralis and isometric leg strength (Tesch & Karlsson, 1978), knee extension strength at a joint angular velocity of 180 deg/s (Thorstensson, 1976) and knee extension strength at 180 deg/s expressed as a percentage of isometric strength (Thorstensson et al, 1976a). In contrast, endurance is correlated with a high percentage of ST fibres (Hulten et al, 1975; Thorstensson & Karlsson, 1976).

On the basis of these findings, one might predict a relatively high percentage of FT fibres within the muscles of "strength" (weight lifters, sprinters, jumpers, throwers) athletes. These athletes have been shown to possess a relatively high (in comparison to endurance athletes) percentage of FT fibres in vastus lateralis (Edstrom & Ekblom, 1972; Gollnick et al, 1972; Haggmark et al, 1978; Karlsson et al, 1975) and deltoideus (Karlsson et al, 1975). It has been suggested (Thorstensson et al, 1977), on the basis of strength (Thorstensson et al, 1976b) endurance (Gollnick *et al*, 1973a) and sprint (Thorstensson *et al*, 1975) training studies and experiments with mono- and dizygous twins (Komi *et al*, 1976), that fibre type distribution (% FT vs % ST) in man is genetically determined and cannot be altered by training.

Biochemistry (enzymes)

Strength (weight lifting, sprinting, jumping, throwing) performance is primarily anaerobic in nature while endurance (e.g. distance running, cross country skiing) is primarily aerobic in nature. Therefore, one might expect strength and endurance athletes to possess relatively high enzyme activity levels for anaerobic and aerobic metabolism respectively. Thus, relatively high levels for creatine phosphokinase (Komi *et al*, 1977) and lactate dehydrogenase (Costill *et al*, 1976; Karlsson *et al*, 1975; Komi *et al*, 1977) but a low level for succinic acid dehydrogenase (Costill *et al*, 1976; Gollnick *et al*, 1972) have been found in strength athletes while the reverse pattern has been observed in endurance athletes (Costill *et al*, 1976; Gollnick *et al*, 1972; Komi *et al*, 1977).

Nervous System

Motor Unit Synchronization

Motor unit synchronization has been shown to be enhanced in weight lifters and in individuals whose occupation involves the performance of brief, forceful muscle contractions (Milner-Brown *et al*, 1975). These results are in agreement with the results of a strength training study discussed above.

Reflex Potentiation

Reflex potentiation has been demonstrated to be enhanced in weight lifters (Milner-Brown et al, 1975) and in elite sprinters (Upton & Radford, 1975); however, one training study failed to show an increase in reflex potentiation (Milner-Brown et al, 1975).

Nerve Conduction Velocity

Kato (1960) and Lastovka (1969) found no difference between athletes and controls in ulnar motor nerve conduction velocity; however, Lastovka (1969) did find a significant difference between athletes and controls in posterior tibial motor nerve conduction velocity. Upton & Radford (1975) found no difference between elite sprinters and controls in median, ulnar or peroneal motor nerve conduction velocity. Variation in the calibre of athletes, type of athlete and extent of training could account in part the variation in results of the different studies.

Motor Unit Counts

Application of a method for estimating the number of motor units within a muscle (McComas et al, 1971) has revealed low motor unit counts in some athletes (McComas, A. J., personal communication). The question arises as to whether the low motor unit counts are due to genetic endowment, the result of the physiological overload associated with training or the result of nerve trauma which occurs in the performance of the sport. In relation to the latter case, Braddom & Wolfe (1978) reported three cases of musculocutaneous nerve injury associated with regular lifting of heavy weights; it was suggested that the coracobrachialis muscle injured the nerve either by intermittent strong contractions or by chronic pressure secondary to hypertrophy; all three subjects recovered when the limb was rested. Injury to the ulnar nerve at the wrist has been reported in cyclists (Eckman et al, 1975), presumably as a result of pressure from the handle bars.

Reflex Time and Reaction Time

Reflex time (Considine, 1966; Karpovich et al, 1960) and reaction time (Beise & Peaseley, 1937; Considine, 1966; Karpovich et al, 1960; Keller, 1942; Knapp, 1961; Olsen, 1956; Slater-Hammel, 1955; Youngen, 1959) have been reported to be shorter in athletes than in control subjects. Sprinters possessed shorter reflex (Lautenback & Tuttle, 1932) and reaction (Westerlund & Tuttle, 1931) times than distance runners.

C. Conclusion

In the present investigation, experiments were designed to extend further the current knowledge (as reviewed above) regarding the effects of strength training and immobilization upon neuromuscular function in man. The rationale for selecting the measures of neuromuscular function used in the investigation is given below.

Previous studies of the effect of training and immobilization upon voluntary strength and of strength performance in athletes have been restricted to the peak force of maximal voluntary contractions. In the present investigation, voluntary strength was also measured as impulse, work, and power.

There has only been one previous study of the effect of strength training upon the contractile properties of human muscle (restricted to twitch tension) and there have been no studies in relation to immobilization. Therefore, changes in twitch tension, contraction time, half relaxation time and rate of tension development were observed following training and immobilization. In addition, the contractile properties of isometric twitch contractions were measured in two groups of strength-trained athletes; namely, gymnasts and weight lifters.

Reflex potentiation has been reported to be enhanced in weight lifters and elite sprinters; however, a short-term training programme involving a few subjects failed to increase reflex potentiation. In the present investigation, more subjects, involving more muscle groups, participated in longer-term strength training programmes to assess the effect of training upon reflex potentiation. Reflex potentiation was also measured in gymnasts and weight lifters. The effect of immobilization upon reflex potentiation was measured for the first time in the present study.

The previously reported data on nerve conduction velocity in athletes have not been uniformly consistent. Therefore, two further groups of athletes were investigated; namely, gymnasts and weight lifters. One previous study revealed no effect of strength training upon motor nerve conduction velocity. In view of the existence of only one previous training study and the inconsistent results in groups of athletes, it was felt that further investigation of the effects of training upon nerve conduction velocity was warranted. The effect of immobilization upon nerve conduction velocity was measured for the first time.

The reduced motor unit counts observed in some athletes raised the question as to whether this would be a wide-spread finding among athletes. The question also arose as to whether the observed low motor unit counts were the result of chronic physiological overload (training) or chronic trauma sustained during training or performance. To provide further data related to these questions, motor unit counts were made in gymnasts and weight lifters, and motor unit counts were made before and after a period of strength training. The effect of immobilization upon motor unit counts was also observed.

In summary, measures of muscle function (contractile properties) and neural function (reflex potentiation, nerve conduction velocity, motor unit counts) were selected to investigate the effects of strength training and immobilization upon neuromuscular function (voluntary strength) in man.

II. METHODS

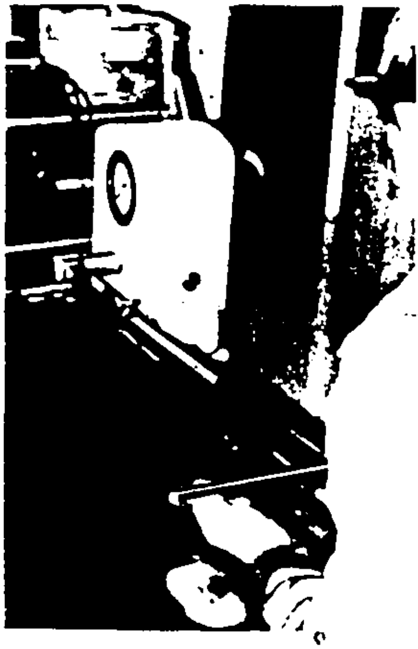
A. Methods of Measurement

1. Voluntary Strength. Voluntary strength was measured with an isokinetic (constant velocity) dynamometer (Cybex II, Lumex Inc., New York). This device allows strength to be measured during isometric and concentric (shortening) muscle contractions. The velocity range of the apparatus is limited and corresponds to 0-210 deg/s (0-3.665 rad/s). The instrument possesses a lever arm, to which various parts of the body may be attached. The lever arm is mechanically prevented from exceeding the preset velocity, and offers resistance equal to the force applied to it by the body part. Thus it is possible, with a single concentric contraction, to measure strength throughout a range of motion.

The muscle groups tested were the ankle plantar flexors, knee extensors, elbow extensors and thumb abductors. The positioning for the strength tests is shown in Figure 1. To test ankle plantar flexion, the subject sat on a chair with the ball of one foot resting on a metal plate. The knee joint was at an angle of approximately 90 degrees (full extension = 0 deg.). The padded lever arm was placed on the thigh at the knee. The subject was instructed to begin each contraction with the plantar flexors relaxed and the ankle joint passively dorsiflexed, and to continue the contraction until the ankle joint was completely plantar flexed. To test knee extension, the subject sat at the end of a padded table, with the edge of the

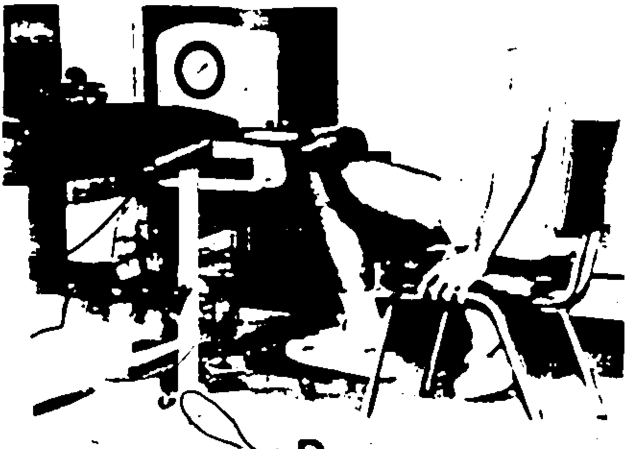
Figure 1. Voluntary strength testing on the Cybex II dynamometer. Positioning of subjects for testing elbow extension (A), Knee extension (B), thumb abduction (C) and ankle plantar flexion (D) is shown. See text for details.

A



C

B



D

table aligned with the knee joint. The thigh of the leg to be tested was restrained by a strap attached to the table. The padded lever arm of the dynamometer was attached to the front of the lower leg. The pivot point ~~of the~~ lever arm was aligned with the knee joint. The subject was instructed to grasp the sides of table and to maintain the trunk in the vertical position. Contractions began with the knee joint at an angle of 90 degrees, and continued until the knee joint was fully extended. To test elbow extension, the subject lay supine upon the padded table. The upper arm of the arm to be tested was restrained by a strap fastened to the table. The padded lever arm was attached to the forearm at the wrist; the pivot point of the lever arm was aligned with the elbow joint. Each contraction began with the elbow joint passively flexed and continued until the joint was completely extended. The forearm was maintained in semi-pronation. To test thumb abduction, the hand was laid supine upon the padded table. The padded lever arm (pad not shown in Figure 1) was placed on the distal phalanx of the thumb. The contractions occurred with the thumb adducted and resting on the index finger.

The velocities selected for testing varied according to the muscle group tested. For elbow extension and knee extension, strength was measured at lever arm velocities of 30 and 180 deg/s. In these two movements, the pivot point of the lever arm was aligned with the respective joints; therefore, the joint angular velocity was equal to the lever arm velocity. For ankle plantar flexion, strength was measured at lever arm velocities of 6 and 36 deg/s. For thumb abduction, strength was measured at a lever arm velocity of 0 deg/s (i.e. isometric contraction).

For all strength tests, subjects were allowed three warm-up contractions followed by three test contractions at each velocity tested. A rest period of 20 seconds was permitted between consecutive test contractions. Subjects were encouraged to make maximal efforts during the test contractions. In each test, the best of the three trials was taken as the measure of strength.

In the course of the experiments, three recorders were used in conjunction with the isokinetic dynamometer. They included a Cybex strip chart recorder (Lumex Inc., New York), a Sanborn 500 strip chart recorder (Hewlett Packard, San Diego, California) and a Hewlett-Packard 7402A oscillograph recorder. Figure 2 shows sample recordings using the Hewlett-Packard recorder. From the recordings of the test contractions, the following mechanical properties could be measured:

(1) Peak torque (N.m, newton-metres) - measured as the peak torque developed during the contraction.

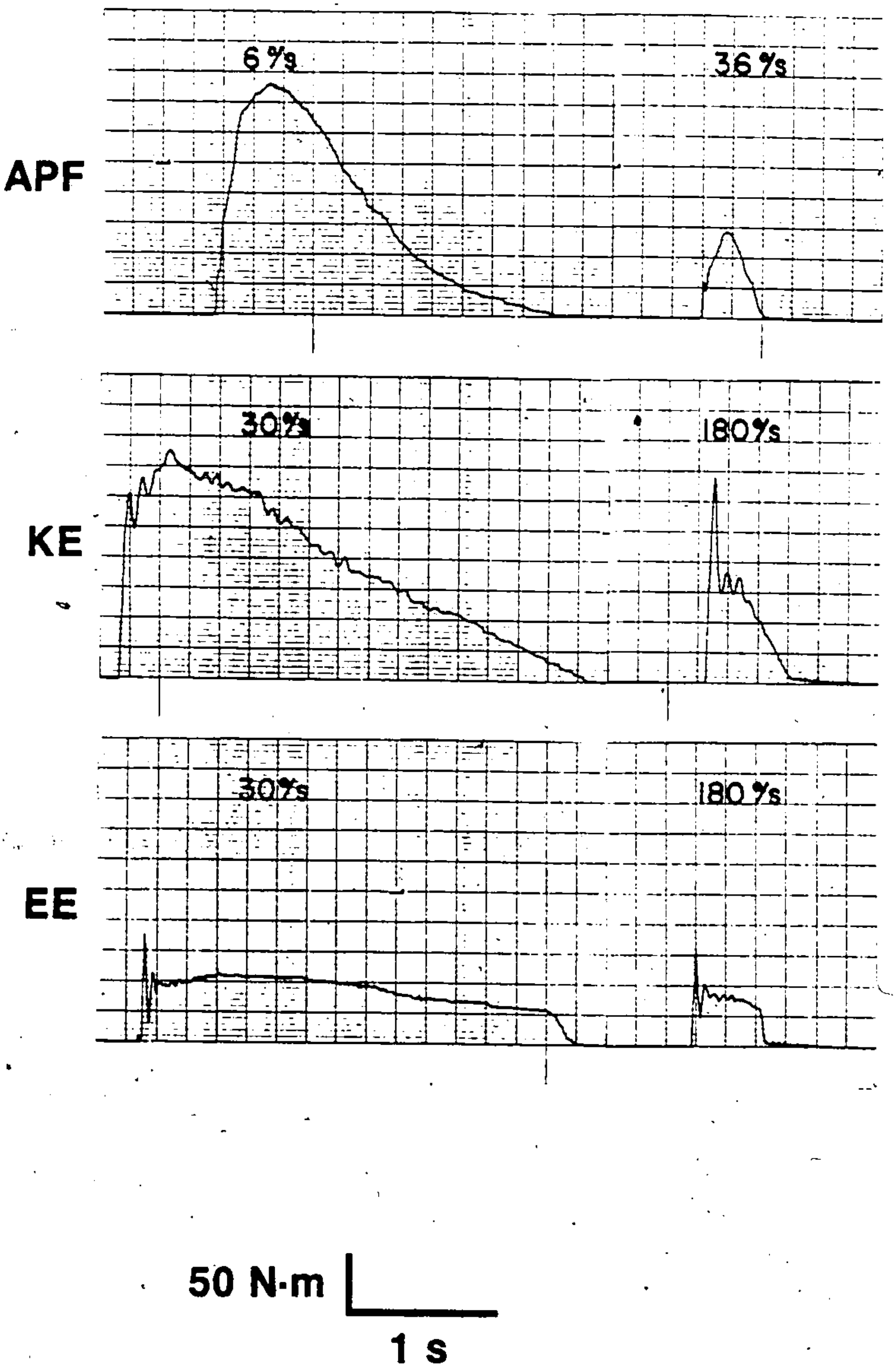
(2) Impulse (N.m.s, newton-metre-seconds) - measured as the area under the torque-time record.

(3) Average torque (N.m) - measured as the impulse divided by the duration of the contraction.

Impulse was measured with a polar planimeter during most of the experimental period. Toward the end of the experimental period, impulse was measured with an electronic integrator.

Values for peak torque, average torque and impulse can be converted to peak power (W, watts), average power (W) and work (J, joules), respectively by multiplying by the lever arm velocity (in rad/s, rad = radians) at which the test contractions were made. In the results of the control experiments, values for all six mechanical properties have been reported. In

Figure 2. Recordings of maximal voluntary concentric contractions performed on the Cybex II dynamometer by a control subject. Recordings of ankle plantar flexion (APF), knee extension (KE) ~~and elbow~~ extension (EE) at the lever arm velocities selected for testing are shown.


APF
6°/s
36°/s
KE
30°/s
180°/s
EE
30°/s
180°/s
50 N·m
1 s

the remaining experiments, only the values for peak torque, average torque and impulse have been reported; however, conversions can be made by multiplying by the appropriate velocity (6 deg/s = 0.1047 rad/s; 30 deg/s = 0.5235 rad/s; 36 deg/s = 0.682 rad/s; 180 deg/s = 3.141 rad/s) in rad/s.

The results of the strength measurements were expressed absolutely and/or per kg body mass.

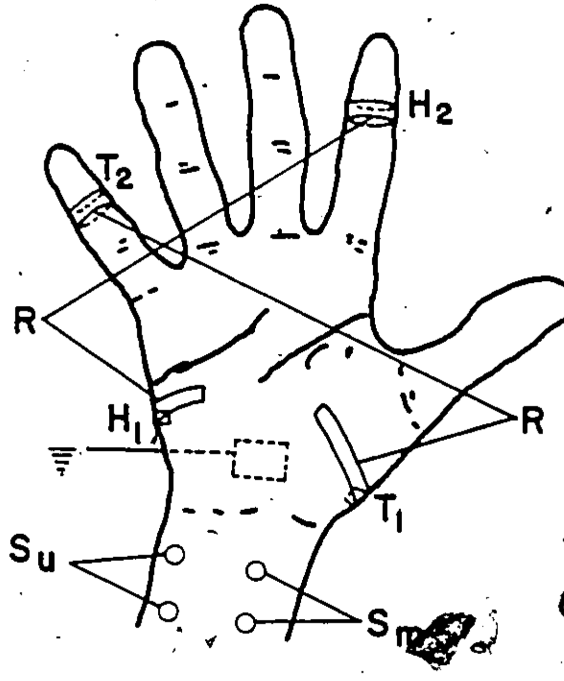
In ankle plantar flexion, knee extension and elbow extension, strength was measured at a relatively low and relatively high velocity. Thus, for each mechanical property, a strength-velocity relation ratio could be determined by dividing the value obtained at the higher velocity by the value obtained at the lower velocity.

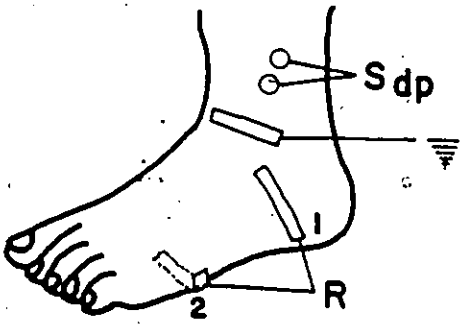
When a muscle group was tested on both left and right sides, a symmetry ratio could be determined for each mechanical property by dividing the value for the weaker side by the value for the stronger side.

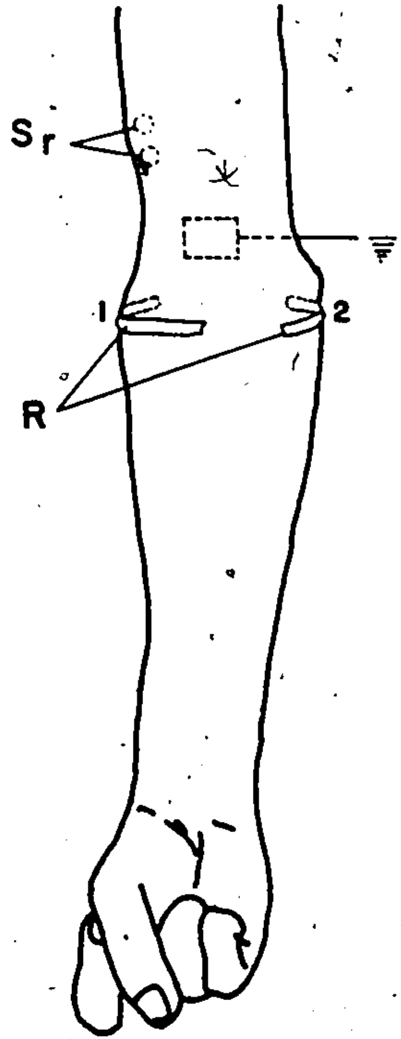
2. Motor Unit Counts. The method for estimating the number of motor units within extensor digitorum brevis (EDB) was that described by McComas et al. (1971), and for estimating the number of motor units within the hypothenar and median invervated thenar muscles, the method described by Sica et al. (1974) was used. The same protocol was used for estimating the number of motor units within soleus (McComas, 1977) and brachioradialis muscles.

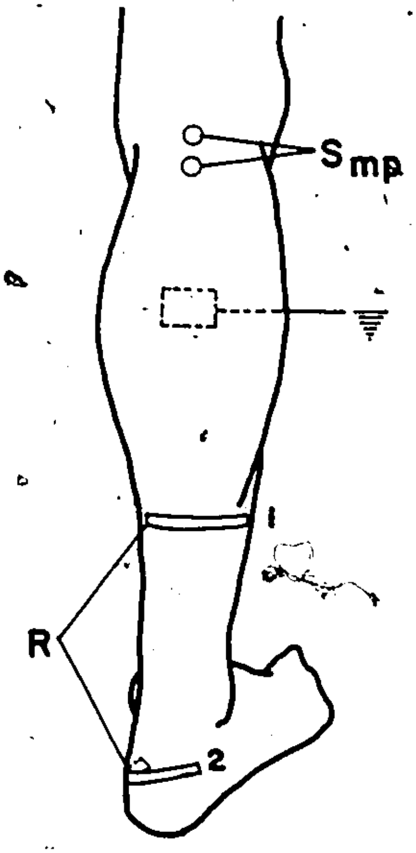
The method involves surface electromyography and graded nerve stimulation. The arrangement of the stimulating and recording electrodes is shown in Figure 3. The stimulating electrodes were

Figure 3. Arrangement of electrodes for estimating the number of motor units within muscles. Median innervated thenar muscles (top left): Sm, median nerve stimulating electrodes; T_1 and T_2, stigmatic and reference recording (R) electrodes. Hypothenar muscles: Su, ulnar nerve stimulating electrodes; H_1 and H_2, stigmatic and reference recording electrodes. Extensor digitorum brevis (top right): S dp, deep peroneal nerve stimulating electrodes; 1 and 2, stigmatic and reference recording electrodes. Brachioradialis (bottom left): Sr, radial nerve stimulating electrodes; 1 and 2, stigmatic and reference recording electrodes. Soleus (bottom right): S mp, medial popliteal nerve stimulating electrodes; 1 and 2, stigmatic and reference recording electrodes. In all cases, the stimulating electrodes were placed with the cathode distal.


H2
T2
R
R
H1
T1
Su
Sm


Sdp
1
2
R


Sr
1
2
R


Smp
1
R
2

chlorided silver discs, 10 mm in diameter, which were mounted in a Perspex holder so that their centres were 3 cm apart. The stimulating electrodes were fastened to the limb by means of a Velcro strap. The stigmatic and reference recording electrodes were strips of silver foil, 6 cm x 6 mm. For EDB, the ground electrode was also a strip of silver foil; however, for the remaining muscles, the ground electrode was a 4 cm x 2.5 cm lead plate. For thenar and hypothenar muscles and EDB, the stigmatic electrode was positioned over the end plate zone. After preparing the skin with alcohol and electrode jelly, the recording electrodes were attached to the skin by adhesive tape.

The stimuli consisted of rectangular voltage pulses 50 or 100 micro seconds in duration, delivered from a Devices Ltd. Model 3072 stimulator which itself received a triggering pulse from a digital timing device (Devices Ltd. Digitimer, Model 3290). The responses were fed through an amplifier using a frequency response which was 3 db down at 2 Hz and 10 kHz. The responses were displayed and measured on a storage oscilloscope with variable persistence (Hewlett-Packard, Ltd., Model 141b).

With the electrodes in place, the subject lay supine or prone upon a bed and was encouraged to relax. Stimuli, which were delivered at a rate of 30 per minute, were gradually increased in intensity from a subthreshold value until the first response appeared. The stimulus intensity was increased further until 8-12 incremental responses had been recorded. The method assumes that each increment in the response reflects the excitation of an additional motor unit. The total amplitude of the responses was measured and a mean motor unit potential amplitude was calculated. The stimulus was then made supramaximal in order to evoke a total muscle response (maximum M wave), whose amplitude was measured. An estimate of the number of motor units within the muscle was made by dividing the value for the amplitude of the total muscle response by the value for the mean motor unit potential amplitude. The method is illustrated in Figure 4. Criticisms which have been raised concerning this method have been discussed in detail by McComas (1977, pp. 307-311).

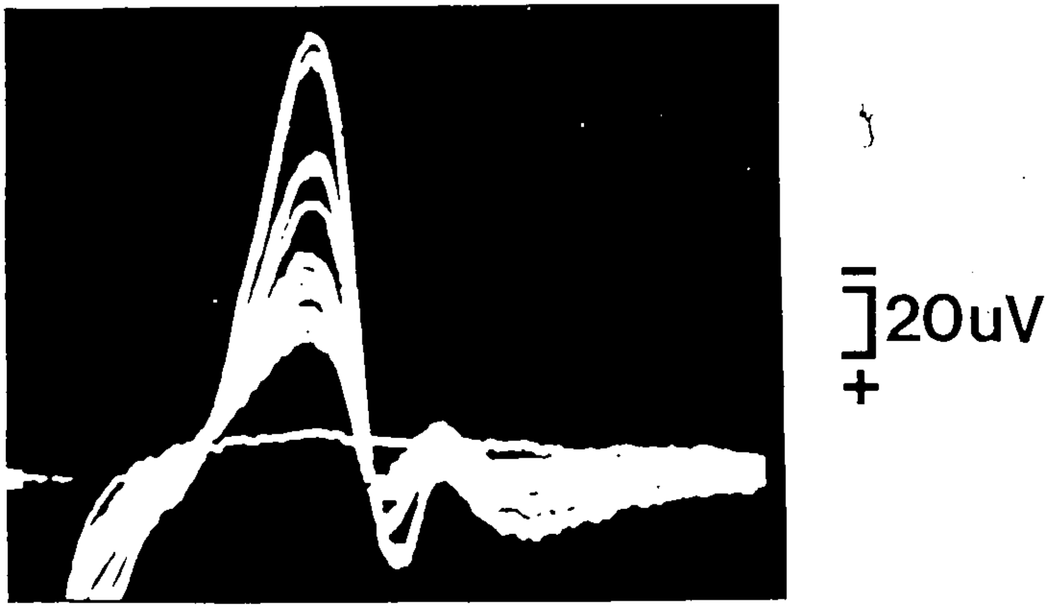
3. Reflex Potentiation. Reflex potentiation was measured using the method described by Upton et al (1971) for thenar, hypothenar and EDB muscles. The same protocol was used to measure reflex potentiation in brachioradialis and soleus muscles.

The arrangement of the stimulating and recording electrodes was the same as for the motor unit counting (Figure 3).

The subject was encouraged to relax and a maximum M wave was elicited by nerve stimulation, and its amplitude was measured. The stimulus was then made supramaximal by 80-100 V, and a series of 10 stimuli were delivered at a rate of 12 per minute. Whenever the response included an F wave, its amplitude was measured. The subject was then instructed to perform 10 maximal contractions of the muscle at a rate of 4 per minute. The contractions were made isometric by the application of external resistance. A stimulus was delivered during each maximal contraction. In all muscles except soleus, the recorded response included a M wave followed by V_1 and V_2 waves (first and second volitional waves respectively). In soleus, the V_2 wave rarely occurred, and results for the V_2 wave in this muscle will not be reported. Examples of V_1 and V_2 responses are shown in Figure 5. The amplitudes of the V_1 and V_2 waves were measured.

From the data obtained by these measurements, potentiation ratios were calculated (see Figure 5). For the V_1 response, a V_1 potentiation ratio was calculated by expressing the mean (of 10 trials)

Figure 4. Estimation of the number of brachioradialis motor units in a 21 year old control subject. At the top are shown 10 incremental responses. In reproduction, the second and third responses appear as one. At the bottom is shown the total muscle response (maximum M wave). Mean increment amplitude, 14.7 uV; maximum M wave, 12 mV; estimated number of motor units, 816.


−
20uV
+

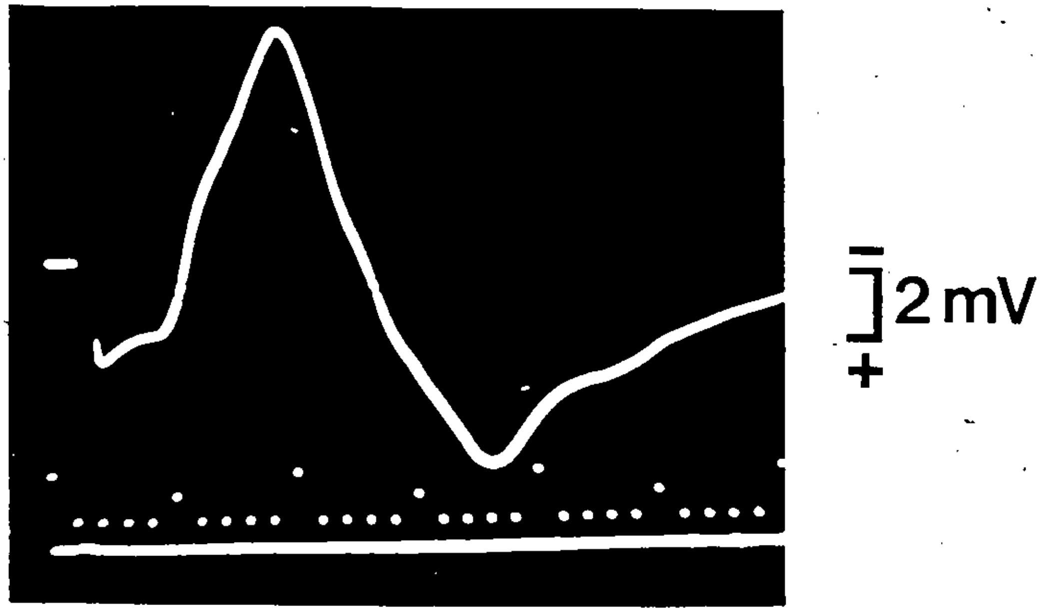
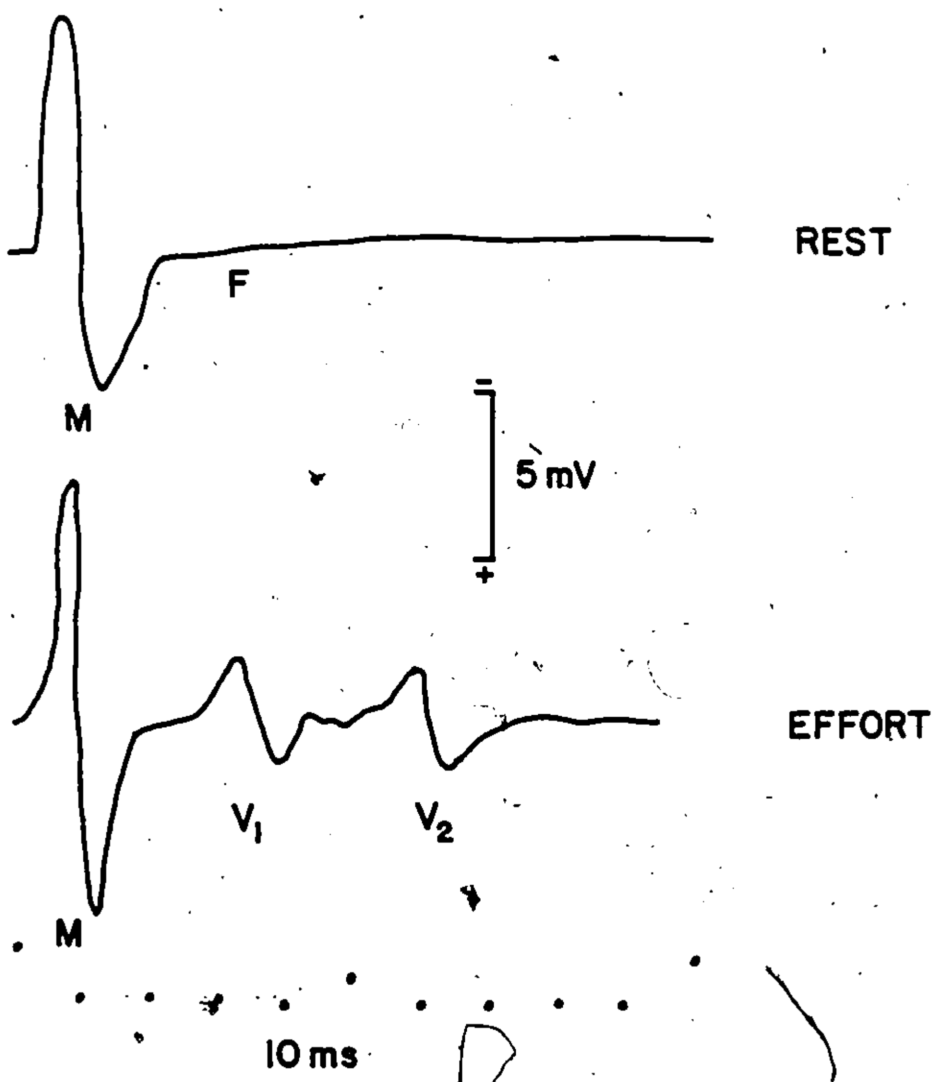

−
2 mV
+

Figure 5. Reflex potentiation in the thenar muscles of a 20 year old control subject. The figure shows hand tracings of actual recordings. The two tracings show responses at rest and during a maximal isometric contraction to supra maximal stimulation of the median nerve. The F wave (F) which often appeared at rest was usually very small and is not resolved at the amplification at which the recording was made. The appearance of the V_1 and V_2 waves during effort is readily seen. At the bottom of the figure are presented the formulae for calculating the reflex potentiation ratios. See text.



POTENTIATION RATIOS

$$V_1 \text{ RATIO} = \frac{V_1 - F}{M} \times 100$$

$$V_2 \text{ RATIO} = \frac{V_2}{M} \times 100$$

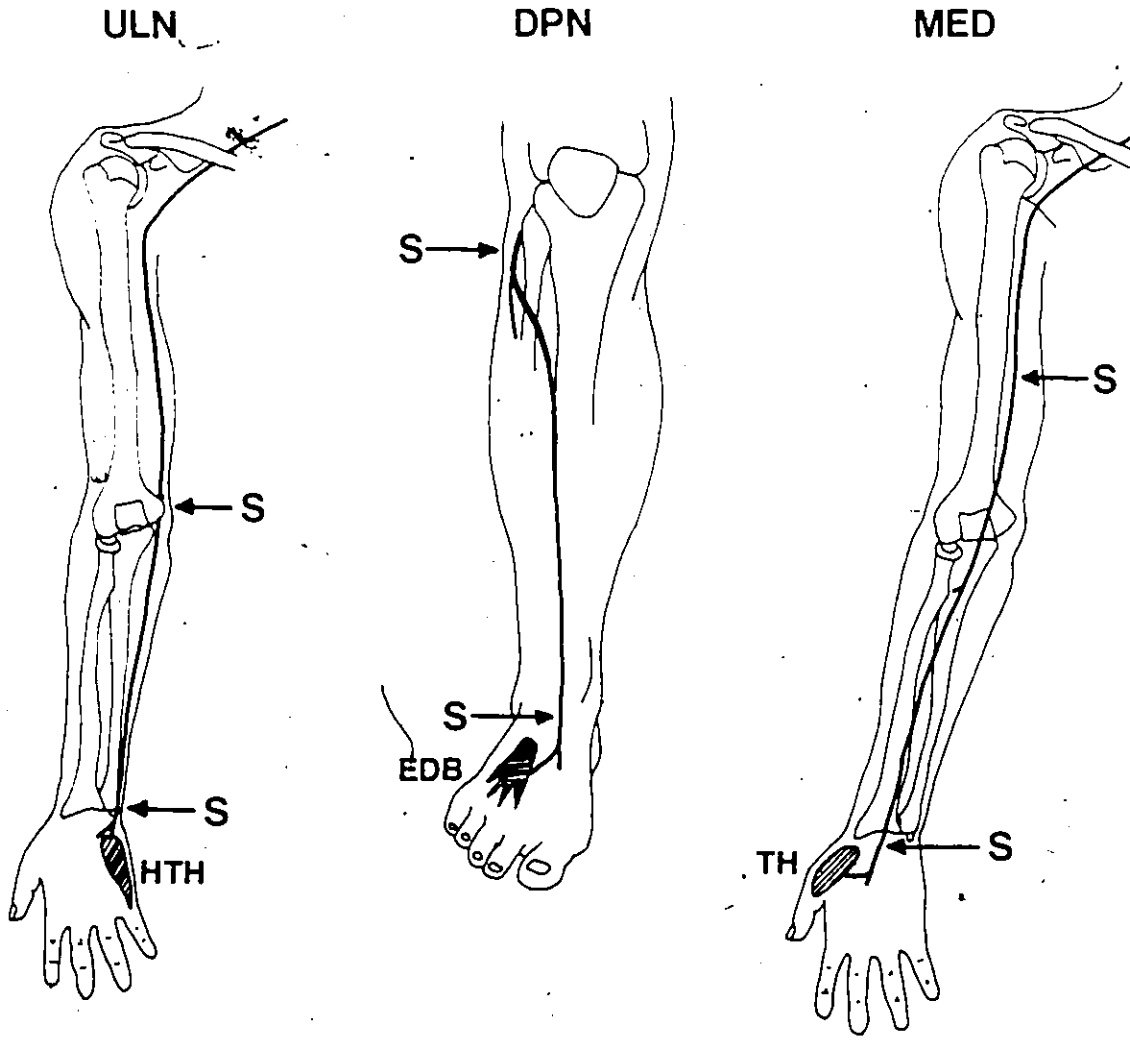
V_1 wave amplitude (minus mean F wave amplitude) as a percentage of the maximum M wave amplitude evoked at rest. Similarly, a V_2 ratio was calculated by expressing the mean V_2 wave amplitude as a percentage of the maximum M wave.

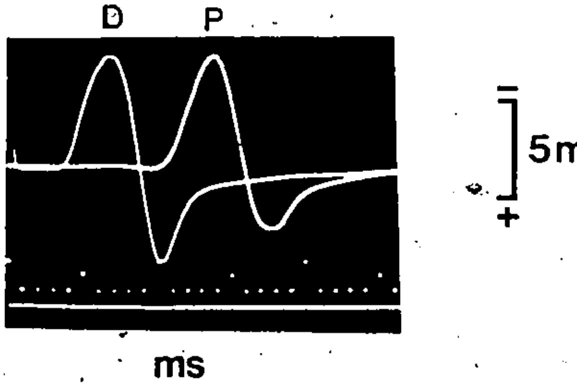
4. Motor Nerve Conduction Velocity. Motor nerve conduction velocity in the median, ulnar and deep peroneal nerves was measured by the conventional method (for example, see Le Quesne, 1971). In this method of estimating the conduction velocity of the most rapidly conducting fibres in a nerve trunk, a supramaximal stimulus is applied to the nerve at two levels and the time interval between the stimulus and the onset of the muscle action potential recorded in both instances. The difference in latency of the two responses is the conduction time in the fastest conducting fibres between the two points stimulated. The difference in latency, together with the distance between the two points, can be used to calculate nerve conduction velocity.

The two levels of stimulation of the median, ulnar and deep peroneal nerves are shown in Figure 6. Latency was measured as the time between the stimulus and the foot of the negative deflection of the muscle action potential. Prior to any measurement of nerve conduction velocity, the limb was warmed (skin temperature = 36-38°C) by means of a heat lamp; this procedure prevented the slowing of nerve conduction velocity that would occur in a cool limb (Le Quesne, 1971).

5. Sensory Nerve Conduction Velocity. Sensory nerve conduction velocity of the median and ulnar nerves was measured

Figure 6. Measurement of motor nerve conduction velocity. Proximal and distal levels of stimulation of the ulnar (ULN), deep peroneal (DPN) and median (MED) nerves are shown; muscle action potentials were recorded from hypothenar (HTH), extensor digitorum brevis (EDB) and thenar (TH) muscles respectively (for arrangement of recording electrodes, see Figure 3). At the bottom of the figure are shown examples of the recorded response in EDB to proximal (P) and distal (D) stimulation of DPN. Response to distal stimulation: amplitude, 9.0 mV; latency, 3.0 ms. Response to proximal stimulation: amplitude, 7.8 mV; latency, 10.0 ms. Calculation of nerve conduction velocity: difference in latency, 7.0 ms; distance between levels of stimulation, 33.6 cm; nerve conduction velocity, 48 m/s.


ULN
DPN
MED
S
S
S
S
S
S
S
EDB
HTH
TH


D
P
−
5mV
+
ms

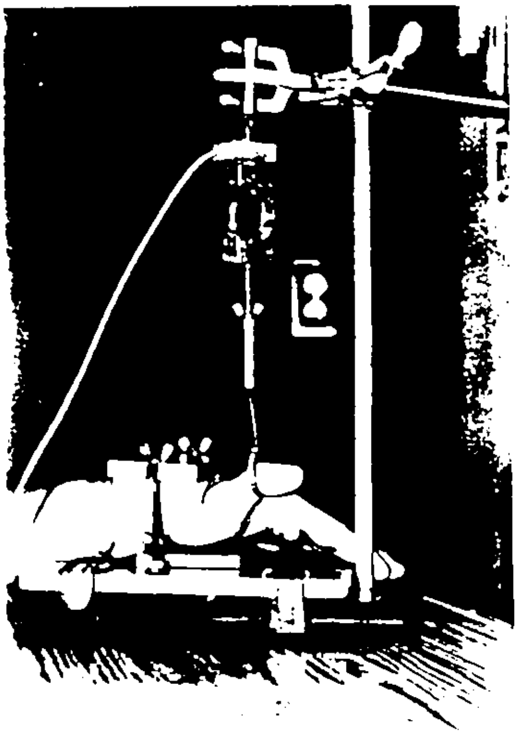
using the method described by McComas et al (1974; see also Cohen and Bramlik, 1976; Goodgold and Eberstein, 1972; Smorto and Basmajian, 1977). The electrodes used for stimulation in the motor unit estimations were used to record the sensory nerve potentials. The electrodes were positioned as shown in Figure 3 to record the orthodromically conducted impulses in digital nerve fibres of the median and ulnar nerves. The stimulating electrodes were two pairs of spring loaded stainless steel clips and were positioned at the base and distal interphalangeal joint of the third (median) and fifth (ulnar) digit (cathode proximal). The amplitude and latency of the sensory nerve potential evoked by supra maximal stimulation were measured. The distance between the cathode and the recording electrode was also measured. The measured distance and the latency were used to calculate sensory nerve conduction velocity.

6. Muscle Twitch Properties. The isometric twitch properties of extensor hallucis brevis, triceps surae and thenar and hypothenar muscles were measured. The properties measured were peak tension, time to peak tension (contraction time) half relaxation time and rate of tension development (peak tension divided by contraction time).

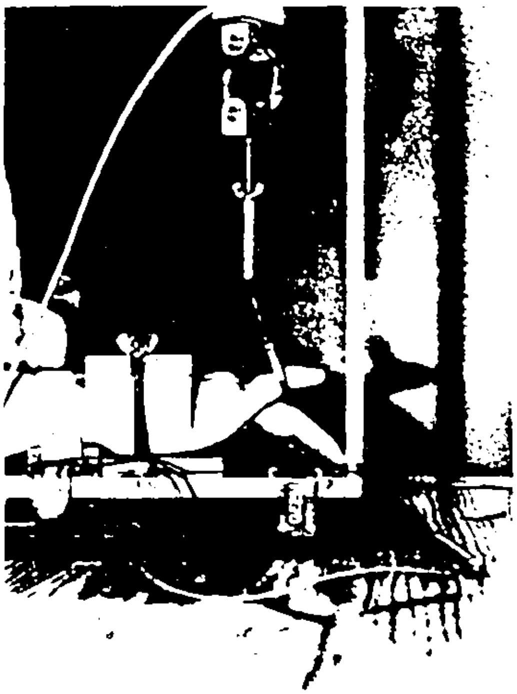
The apparatus and set-up for measuring the twitch properties are shown in Figure 7. To measure the twitch properties of extensor hallucis brevis, the method described by Sica and McComas (1971) was used. The foot was positioned in an adjustable holder. The sole of the foot rested against a flat aluminum plate containing a window, through which the great toe could be protruded and connected to a strain gauge (Statham type G1-80-350, Gould Inc., Oxnard, California). The strain gauge was attached by a wire hook to a copper ring round the proximal phalanx of the great toe. The strain gauge was mounted in a U-shaped bar which pivoted about an axis aligned with the first metatarso phalangeal joint. The resonant frequency of this apparatus was 2.2 KHz and the compliance was 5 um/N. A 9.81 N (1 kg) initial tension was placed on the muscle by moving the U-bar. A stimulator probe type 202375 (Rochester Electro-Medical Inc., New Hope, Minnesota), placed on the skin over the lateral branch of the deep peroneal nerve at the medial border of EDB, was used for stimulation (cathode distal). A supra maximal stimulus was used to evoke the twitch response.

To measure the twitch properties of the thenar and hypothenar muscles, the hand was placed palm down on the base of a retort stand. A padded wood plate was pressed firmly onto the back of the hand and fastened securely to the retort stand. The ring of a ring strain gauge type 412500 (Rochester Electro-Medical Inc.) was placed round the distal interphalangeal joint of the thumb (thenar) or fifth (hypothenar) finger. The strain gauge was held by a retort stand clamp. The resonant frequency of this apparatus was 400 Hz and the compliance was 7 um/N. The height of the clamp could be adjusted to place an initial tension of 9.81N upon the muscle. The arrangement for stimulating the median (thenar) and ulnar (hypothenar) nerves was the same as for the motor unit counting (Figure 3). A Supra maximal stimulus was used to evoke the twitch response.

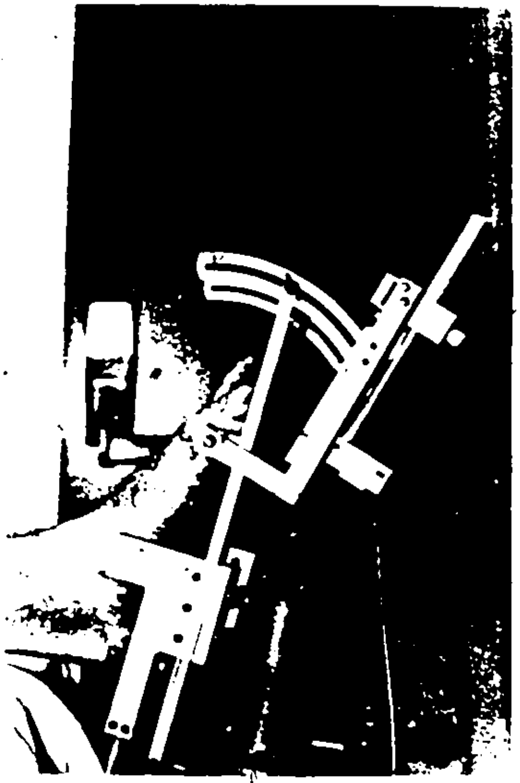
Figure 7. Apparatus and set-up for the measurement of muscle twitch properties in thenar (A), extensor hallucis brevis (B), hypothenar (C) and triceps surae (D). See text.



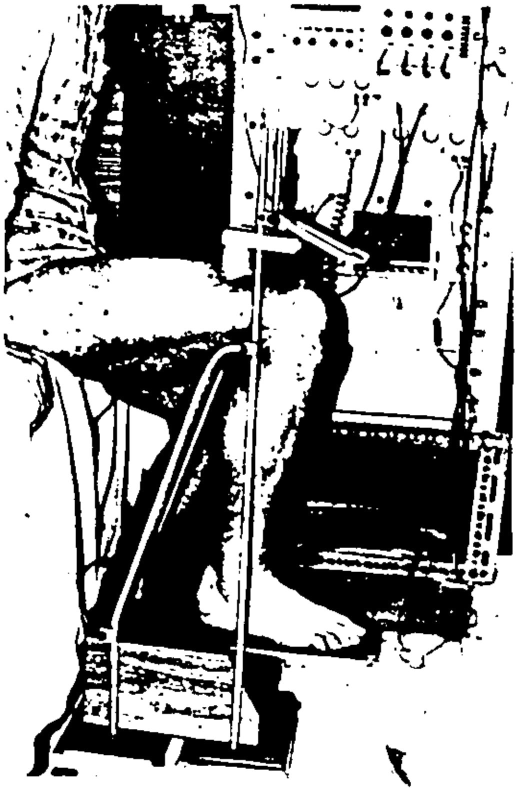
A



C



B



D

To measure the twitch properties of the triceps surae muscle, the subject sat with the thigh horizontal and the knee joint at an angle of approxmiately 90 degrees. The foot was placed on an ankle jerk strain gauge type 415005 (Rochester Electro-Medical, Inc.). The resonant frequency of this apparatus was 45 Hz and the compliance was 45 um/N. The positioning of the foot on the strain gauge was the same for each subject. The strain gauge rested on a stand, one feature of which was a padded wood plate which could be pressed down firmly on the thigh at the knee and secured. This arrangement prevented raising of the heel during contraction of the calf muscles. The stimulator probe (cathode distal) was placed in the popliteal fossa in order to stimulate the medial popliteal nerve. A supra maximal stimulus was used to evoke the twitch response.

Prior to evoking a twitch response, the muscle was warmed with a heat lamp until the temperature of the skin overlying the muscle could be maintained at 36 to 38 degrees C. Prior to each measurement, the system was calibrated with a 1 kg mass.

All of the strain gauges were energized by a 7 volt d.c. power supply which was connected to a low noise differential d.c. amplifier. The display device was the storage oscilloscope described above.

7. Anthropometry. Height and body mass were measured to the nearest 1.0 cm and 0.1 kg respectively. Upper arm, thigh, and calf girth measurements were made at the level of greatest circumference to the nearest 1.0 mm with a steel tape.

B. Control Experiments

The control experiments consisted of collecting data on samples of control subjects using the measurements described above.

For voluntary strength measurements of ankle plantar flexion, knee extension and elbow extension, 25 males, aged 18-46 years ($\bar{X}$, 24.3; SD, 7.3) served as subjects. The subjects included university students, faculty and staff. In these same subjects, the anthropometric measurements were also made.

The characteristics of the control subjects on whom electrophysiological measurements were made are presented in Table 1. The subjects included university students and staff.

All control subjects were healthy at the time of investigation and were unpaid volunteers who participated with their own informed consent.

C. Training and Immobilization Experiments

1. Immobilization. Fourteen male subjects underwent immobilization. Thirteen of the subjects ranged in age from 19-23 years ($\bar{X}$, 20.1; SD, 1.0). The fourteenth subject was 44 years of age. The subjects were paid volunteers who participated with their own informed consent. The casting procedure was approved by the ethics committee of McMaster University's Department of Medicine. The thumb and elbow joint (joint angle approximately 120 deg.) were immobilized by placing the non-dominant arm in a fibreglass (Lightcast II, Merck & Co., West Point, Pa.) cast (Figure 8). The duration of immobilization ranged from 3-7 weeks ($\bar{X}$, 4.7; SD, 1.0). Measurements made before and after (within two hours) immobilization included voluntary strength of elbow extension (at a velocity of 30 deg/s on the Cybex), voluntary strength of thumb abduction (isometric contractions on the Cybex), median motor nerve conduction velocity and motor unit counts, reflex potentiation and the muscle twitch properties of the median-innervated thenar muscles.

Twelve subjects underwent both immobilization and training. Six

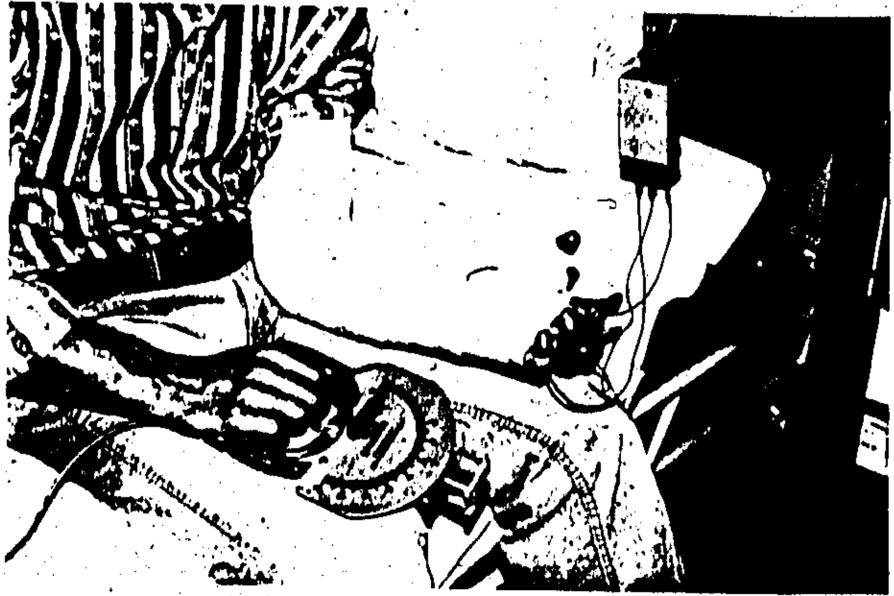
TABLE 1. Age and sex of control subjects on whom electrophysiological measurements were made.

Measure	N			Age		
	Male	Female	Total	X̄	SD	Range
Motor unit counts						
Brachioradialis	45	3	48	22.0	2.3	18-30
EDB	19	6	25	22.3	3.3	19-32
Hypothenar	13	1	14	21.1	2.1	19-27
Soleus	37	6	43	21.9	2.5	19-30
Thenar	25	1	26	21.9	5.2	19-44
Reflex potentiation						
Brachioradialis	33	2	35	22.0	2.3	18-30
EDB	12	4	16	22.1	2.8	19-30
Hypothenar	11	2	13	20.7	1.4	19-24
Soleus	23	6	29	21.8	3.5	19-27
Thenar	25	3	28	21.3	4.7	19-44
Motor nerve conduction velocity						
DPN	18	6	24	22.5	3.5	19-30
Median	30	1	31	22.0	4.8	19-44
Ulnar	12	1	13	21.2	2.3	19-27
Twitch properties						
EHB	1	4	5	20.0	0.7	19-21
Hypothenar	15	4	19	21.6	2.8	19-30
Thenar	18	1	19	21.2	5.6	19-44
Triceps surae	46	10	56	22.2	3.1	19-32

Figure 8. Method of immobilization. A: the cast used to immobilize the thumb and elbow joint. A small opening in the cast permitted placement of a recording electrode on the skin overlying the thenar muscles. B: arrangement for recording from the thenar muscles of the immobilized limb while performing muscle contractions with other muscle groups.

A

B



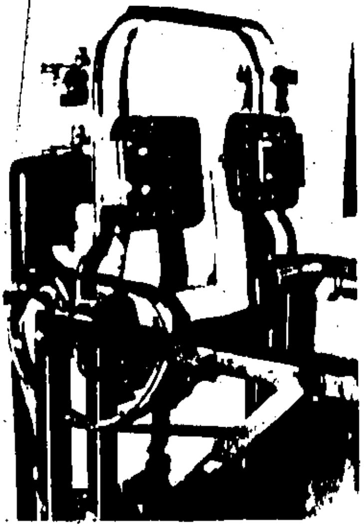
subjects immobilized prior to training, and the other six subjects trained prior to immobilization. Measurements were made in the control condition and after training and immobilization. In the two subgroups (to which subjects had been randomly assigned), mean (± SD) duration of immobilization (5.1 ± 1.2 and 4.8 ± 0.6 wks) and training (20.3 ± 3.8 and 16.8 ± 3.3 wks) was similar.

An additional subject, C.C., aged 21 years, who had sustained a fracture of the humerus, was investigated after 6 weeks of immobilization, after 12 weeks of recovery and after 20 weeks of training.

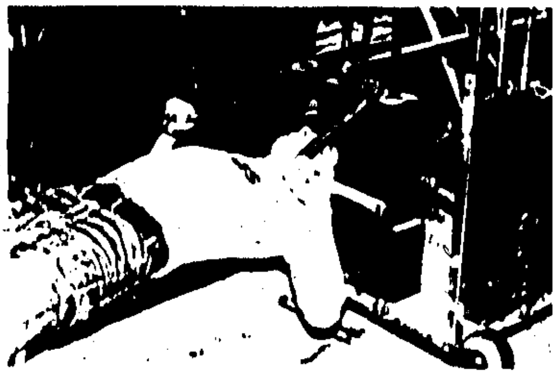
In three subjects who underwent immobilization, a small opening was made in the cast so that a recording electrode could be placed on the skin overlying the thenar muscles (Figure 8). The overall arrangement of the recording electrodes was as shown in Figure 3. While resting the immobilized limb, the subjects were instructed to contract other muscle groups (finger flexors and elbow flexors of the contra lateral limb) at various percentages of maximal voluntary strength and with different durations. The subjects were also instructed to tie their shoe laces using the fingers of the immobilized limb. During these activities, electromyographic recordings were made from the thenar muscles. Observations were made on one subject after one week of immobilization and on the other two subjects after five weeks of immobilization.

2. <u>Training</u>. The training was designed to increase the force of maximal voluntary contractions (i.e. strength training). The training methods included weight lifting, isometric contractions and concentric contractions on the Cybex. The muscles trained were triceps (elbow extension), brachioradialis (elbow flexion), triceps surae (ankle plantar flexion), EDB (extension of the toes), thenar muscles (thumb abduction) and hypothenar muscles (flexion of the fifth finger). Illustrations of some of the weight lifting exercises used in the training are shown in Figure 9.

Figure 9. Some of the weight lifting exercises used for strength training. To train elbow extension, the Nautilus elbow extension unit (A), the bench press (B), the press down (C) and the weighted dips (D) were used. E: the seated heel raise for training the ankle plantar flexors. F: weight lifting apparatus used to train thumb abduction; the same apparatus was used to train flexion of the fifth finger.

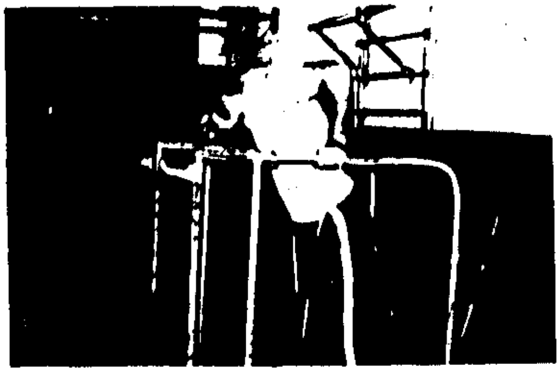


A



B

C



D

E

F

All of the subjects (N=14) who trained elbow extension performed the weight lifting exercises illustrated in Figure 9 (A-D). The exercises were performed three times per week. In two of the weekly training sessions, 3-5 sets of 6-10 repetitions of each exercise were performed (a repetition is one execution of an exercise movement, and a set is a group of consecutive repetitions, followed by a rest period). The interset rest period was two minutes. For each exercise, a weight was selected which permitted no more than the designated number of repetitions to be completed, despite maximal effort. In the first 2-3 weeks of training, subjects performed 3 sets of each exercise; thereafter, 5 sets of each exercise were performed. In each exercise, subjects were instructed to select a weight which initially permitted only 6-7 repetitions to be performed on the first set; when 10 repetitions could be performed on the first set, the weight was increased and the process repeated. The exercises were performed slowly through the greatest possible range of movements (i.e. "good style"). Elbow extension exercises were performed at a velocity similar to the velocity employed for testing and training on the Cybex (see below). In the third weekly training session, the "pyramid" system was performed. In the "pyramid" system, the weight is increased after each set until on the final set, only one repetition can be performed. Six of the subjects also trained elbow extension on the Cybex (Figure 1A). This training consisted of two sets of 10 maximal concentric contractions at a joint angular velocity of 30 deg/s. The contractions were performed at a rate of four per minute; there was a two minute rest period between the two sets. The training was performed three times per week.

To train ankle plantar flexion, subjects (N=7) performed the weight lifting exercise shown in Figure 9E using the same procedure described above for training elbow extension.

To train the thenar muscles (thumb abduction), eight of the 14 subjects who trained this movement performed the weight lifting exercise shown in Figure 9F, using the same procedure described above for elbow extension. The remaining six subjects trained by performing isometric contractions on the Cybex (Figure 1C). In this training, subjects performed two sets of ten maximal, five second, isometric contractions at a rate of four per minute, with a two minute rest period between the sets. The training was performed three times per week.

To train the hypothenar muscles (flexion of the fifth finger), subjects (N=3) used the weight lifting apparatus shown in Figure 9F. The training consisted of performing flexion of the fifth finger using the procedure described above for elbow extension. The training occurred three times per week.

To train extensor digitorum brevis (EDB), subjects (N=3) attempted to extend the toes against an external resistance which caused the contractions to be isometric. Two sets of ten maximal, five second, isometric contractions were performed at a rate of four per minute, with a two minute rest period between the sets. The training occurred three times per week.

To train elbow flexion (brachioradialis) subjects (N=4) performed elbow flexion (forearm semi-pronated) with a dumbbell according to the weight training procedure described for elbow extension.

The mean (±SD) duration of training was for elbow extension (triceps), 19.0 ± 3.8 wks; ankle plantar flexion (triceps surae), 21.1 ± 2.4 wks; thumb abduction (thenar muscles), 18.1 ± 4.8 wks; flexion of the fifth finger (hypothenar muscles), 21.2 ± 1.1 wks; extension of the toes (EDB), 9.3 ± 1.5 wks; elbow flexion (brachioradialis), 10.7 ± 6.1 wks.

For elbow extension (triceps) and thumb abduction (thenar muscles), the measurements made before and after training were the same as in the immobilization experiments described above. The before and after training measurements for the other muscles were for triceps surae: soleus motor unit counts and reflex potentiation and muscle twitch properties; brachioradialis: reflex potentiation; hypothenar muscles: motor unit counts, reflex potentiation, muscle twitch properties and motor nerve conduction velocity of the ulnar nerve; EDB: motor unit counts, reflex potentiation, muscle twitch properties and motor nerve conduction velocity of the deep peroneal nerve (DPN).

The subjects who participated in the training experiments consisted of 18 male and 2 female university students, ranging in age from 19-24 years (X̄, 20.6; SD, 1.4). The subjects included paid and unpaid volunteers who participated with their own informed consent.

D. Voluntary Strength and Electrophysiological Measurements in Weight Trainers

Voluntary strength and electrophysiological measurements were made in seven competitive weight lifters, four body builders and six unclassified weight trainers. This entire group of subjects, who will be called weight trainers or weight lifters, consisted of males ranging in age between 20-35 years (X̄, 25.8; SD, 4.4). These subjects were paid volunteers who participated with their own informed consent. Voluntary strength of ankle plantar flexion, knee extension and elbow extension was measured on the Cybex. Height, body mass and upper arm, calf and thigh girth were also measured. Electrophysiological measurements included motor unit counts and reflex potentiation of soleus and the median innervated thenar muscles, muscle twitch properties of triceps surae and the median innervated thenar muscles and the motor nerve conduction velocity of the median nerve.

The results of the measurements in the weight trainers were compared with the corresponding results in groups of male control subjects.

E. Electrophysiological Measurements in Gymnasts

Electrophysiological measurements were made in five female gymnasts, age 12-14 years (X̄, 13.0; SD, 0.7) and eight male gymnasts aged 20-27 years (X̄, 23.3; SD, 2.7). All subjects were unpaid volunteers who participated with their own informed consent. For subjects below the age of 18 years, parental consent was also received. The measurements included motor unit counts (EDB, thenar, hypothenar, soleus and brachioradialis), reflex potentiation (EDB and brachioradialis), motor nerve conduction velocity (median, ulnar, deep peroneal) sensory nerve conduction velocity (median, ulnar) and muscle twitch properties (triceps surae). It was not possible to perform all of the measurements on every gymnast (see RESULTS).

The results of the measurements in the gymnasts were compared with the corresponding results in groups of control subjects.

F. Knee Extension Strength in Athletes

Knee extension strength was measured in four groups of male athletes: the weight lifters described above (N=12); three members of the Canadian national sprint team in 1976; the Canadian national cross country ski team in 1975 (N=5); the Ontario provincial cycling team in 1975 (N=5).

The results of the measurements were compared with the corresponding results in a group of male control subjects.

G. Statistical Methods

Descriptive statistics included the mean ($\bar{X}$), standard deviation (SD), standard error of the mean (SE), range (min-max) and the number of subjects or cases (N).

Comparisons between groups were made with the t-test (two-tailed) for independent groups. When measurements were repeated in the same group of subjects, the t-test (two-tailed) for non-independent groups was used.

Correlations between pairs of variables were computed by the Pearson product-moment method (r).

Levels of significance (p) were indicated as non-significant (NS) and significant at $p < 0.05$, $p < 0.025$, $p < 0.02$, $p < 0.01$, $p < 0.005$

and $p < 0.001$. The significance level of $p < 0.10$ was indicated as: NS, $p < 0.10$.

Reproducibility of the measurements was determined by two methods. When a measurement was performed on subjects on several different occasions, the mean, standard deviation and coefficient of variation (V) of the results of the repeated measurements were computed. The coefficient of variation was used as the indication of reproducibility.

When a measurement was made only twice in a group of subjects reproducibility was determined by computing the "method error" using the following formula (Friman, 1977; Thorstensson, 1976):

$$ME = \sqrt{\Sigma(d-\bar{d})^2/2(n-1)}$$

in which d = the difference between the two measurements in each subject, $\bar{d}$ = the mean difference and n = the number of subjects. The method error (ME) has been defined as the standard deviation for a single experiment (Thorstensson, 1976) and may be expressed in the units of measurement or as a coefficient of variation by using the following formula:

$$ME(V) = \frac{ME}{(\bar{X}_1+\bar{X}_2)/2} \times 100$$

in which ME(V) = the method error, expressed as a coefficient of variation, ME = the method error, $\bar{X}_1$ = the mean result of the group of subjects on the first testing occasion and $\bar{X}_2$ = the mean result on the second testing occasion.

III. RESULTS

A. Reproducibility of Measurements

1. Voluntary Strength. The method error for the measurement of ankle plantar flexion, knee extension and elbow extension strength is given in Table 2 . The overall method error for these measurements was 11.5%. There was some variation in the method error according to the movement (ankle plantar flexion, 14.6%; knee extension, 8.3%; elbow extension, 7.9%), the mechanical property (peak torque and power, 11.2%; average torque and power, 10.4%; impulse and work, 11.3%), the velocity (slow, 9.3%; fast, 12.6%) and the side (left, 14.5%; right, 11.4%) measured. When the order at which the velocities were tested was reversed on the second testing session, the method error (12.0%) was similar to when the same order of velocities was used on the second occasion (12.5%).

The overall method error for the determination of the strength-velocity relation was 13.2%. There was some variation in the method error with respect to the movement (ankle plantar flexion, 14.6%; knee extension, 8.3%; elbow extension, 7.9%), the mechanical property (peak torque and power, 13.7%; average torque and power, 12.1%; impulse and work, 13.7%) and the side (left, 16.7%; right, 12.0%).

The overall method error for the determination of the symmetry ratio was 10.1%. There was some variation with respect to the movement (ankle plantar flexion, 12.4%; elbow extension, 7.8%), the mechanical property (peak torque and power, 8.0%; average torque and power, 8.3%;

TABLE 2. Reproducibility of voluntary strength measurements made on two separate days

Movement	Velocity deg/s	Side	Method error (V), %		
			Peak torque Peak power	Average torque Average power	Impulse Work
Ankle plantar flexion (N = 15)	6	left	11.5	14.5	11.8
		right	9.7	11.9	18.4
	36	left	21.7	20.2	22.7
		right	13.3	12.4	16.0
	36/6	left	21.7	16.4	19.8
		right	15.2	12.9	21.3
Knee extension (N = 13)	30	right	5.9	6.8	5.2
	180	right	9.2	5.7	6.6
	180/30	right	12.3	12.4	10.5
Elbow extension (N = 11)	30	left	9.7	7.3	6.8
		right	7.1	6.5	7.1
	180	left	15.6	9.2	8.5
		right	8.3	9.1	10.1
	180/30	left	14.5	8.2	9.3
		right	4.7	10.5	7.5

impulse and work, 12.6%) and the velocity (slow, 9.0%; fast 10.1%; strength-velocity relation, 10.7%).

In the training and immobilization experiments, voluntary isometric muscle strength of thumb abduction was measured. The method error of this measurement, determined from repeated measurements in seven subjects, was 9.4%.

2. Motor Unit Counts. The overall method error of the motor unit counting measurement was 26.4%. The method error varied in different muscles (see Table 3). In brachioradialis and soleus muscles, reproducibility of this measurement was also determined by testing a group of subjects on several different occasions (Table 4). The average coefficient of variation was 19.2% for brachioradialis (N=7) and 18.0% for soleus (N=2). In these two muscles, the two methods of determining reproducibility of measurement produced similar results.

The method error for the measurement of the maximum M wave amplitude in the various muscles is presented in Table 3. In each muscle, the method error for M wave amplitude was smaller than for the motor unit counts. In brachioradialis and soleus muscles, reproducibility of this measurement was also determined by testing a group of subjects on several different occasions (Table 4). In this group of subjects, the method error for M wave amplitude was not consistently smaller than the method error for the motor unit counts.

3. Motor Nerve Conduction Velocity. The overall method error for this measurement was 3.4%. The variation in method error in the different nerves tested is shown in Table 5.

4. Reflex Potentiation. The overall method error for the V_1/M x100 measurement was 28.1%, and for the V_2/Mx100 measurement, 26.9%. Variation of the method error in different muscles is shown in Table 6.

5. Muscle Twitch Properties. The method error for the measurement of muscle twitch properties is presented in Table 7. The overall method

Table 3. Reproducibility of motor unit counts and maximum M wave amplitude as indicated by the method error calculated from duplicate determinations

Muscle	N	Method Error (V), %	
		Motor Unit Counts	M Wave Amplitude
Brachioradialis	30	24.0	19.2
Extensor digitorum brevis	13	29.6	16.6
Hypothenar	7	26.8	3.6
Thenar	27	22.6	9.9
Soleus	21	22.0	7.6

Table 4. Reproducibility of motor unit counts and maximum M wave amplitude in brachioradialis and soleus muscles in subjects who were tested on several occasions

Muscle	Subject	Number of tests	Coefficient of Variation (V), %	
			Motor unit counts	Maximum M wave amplitude
Brachioradialis	LR	9	25.7	16.3
	BB	10	11.1	14.6
	BW	10	18.8	27.4
	DN	8	23.6	14.4
	GB	6	12.7	18.1
	PL	7	34.0	28.4
	JW	4	15.1	15.5
Soleus	DF	9	30.6	11.1
	EN	4	5.3	7.2

Note: Each test was performed on a separate day.

TABLE 5. Reproducibility of measurement of motor nerve conduction velocity.

		Motor nerve conduction velocity (m x s^{-1})		
Nerve	N	$\frac{\bar{x}_1 + \bar{x}_2}{2}$	ME	ME (V) %
Deep peroneal	11	48.8	2.7	5.5
Median	20	59.8	1.9	3.2
Ulnar	5	56.8	0.8	1.4

TABLE 6. Reproducibility of measurement of reflex potentiation.

Muscle	N	$V_1/M \times 100$			$V_2/M \times 100$		
		$\frac{\bar{x}_1 + \bar{x}_2}{2}$	ME	ME (%)	$\frac{\bar{x}_1 + \bar{x}_2}{2}$	ME	ME(V) %
Brachioradialis	15	31.6	6.5	20.5	23.1	5.0	21.7
Extensor digitorum brevis	5	16.4	7.5	45.7	27.4	8.9	32.6
Hypothenar	4	19.4	5.1	26.2	16.4	3.9	23.8
Thenar	22	26.3	5.3	20.2	23.7	6.9	29.3
Soleus	13	16.3	4.6	27.9	–	–	–

Note: in the soleus, the $V_2/M \times 100$ measurement was not made

TABLE 7. Reproducibility of measurement of muscle twitch properties.

		Method error (V), %			
Muscle	N	Twitch tension	Contraction time	Rate of tension development	Half relaxation time
Extensor hallucius brevis	5	11.3	12.3	18.4	12.1
Hypothenar	5	37.1	3.0	30.9	12.0
Thenar	17	11.5	8.5	14.3	15.2
Triceps surae	16	5.6	8.1	8.7	6.1

error for extensor hallucis brevis was 13.5%, for hypothenar, 20.8%, for thenar, 12.4% and for triceps surae, 7.1%. The method error varied according to the twitch property measured (twitch tension, 16.4%; contraction time, 8.0%; rate of tension development, 18.1%; half relaxation time, 11.4%).

6. Anthropometric Measurements. The method error for the anthropometric measurements is presented in Table 8.

7. Summary. A summary of the reproducibility of the measurements is presented in Table 9. The method error was smallest for the anthropometric measurements and motor nerve conduction velocity, was largest for the motor unit counts and reflex potentiation, and was intermediate in magnitude for voluntary strength and twitch properties.

B. Control Measurements

1. Voluntary Strength. The results of the voluntary strength measurements are presented in Tables 10-12. On the average, the values for the right side were 6.6±4.1% ($\bar{x}$±SD) greater than those for the left side. There was some variation according to the movement (ankle plantar flexion, 4.7±4.1%; knee extension, 8.7±2.5%; elbow extension, 6.3±4.9%), the mechanical property (peak torque and power, 7.6±4.2%; average torque and power, 4.2±4.2%; impulse and work, 7.9±3.4%) and the velocity (slow, 4.5±3.9%; fast, 8.7±3.2%). The values for average torque and power were, on the average, 62.0±9.8% of those for peak torque and power. There was some variation according to the movement (ankle plantar flexion, 57.5±2.0%; knee extension, 54.1±4.7%; elbow extension, 74.3±3.6%), the side (left, 63.1±11.2%; right, 60.8±9.0%) and the velocity (slow, 64.4±9.2%; fast, 59.5±10.6%).

The correlations among the mechanical properties are presented in Table 13. All correlations were positive and statistically significant.

TABLE 8. Reproducibility of anthropometric measurements.

Measure	N	Method error (V), %
Body mass	14	0.8
Calf girth	15	0.5
Thigh girth	15	1.7
Upper arm girth	15	1.1

TABLE 9. Summary of reproducibility of measurements.

Measure	Method error (V), %
Voluntary strength	
Peak torque and power	11.2
Average torque and power	10.4
Impulse and work	11.3
Strength-velocity relation	13.2
Symmetry ratio	10.1
Motor Unit counts	26.4
Motor nerve conduction velocity	3.4
Reflex potentiation	
$V_1/M \times 100$	28.1
$V_2/M \times 100$	26.9
Twitch properties	
Twitch tension	16.4
Contraction time	8.0
Rate of tension development	18.1
Half relaxation time	11.4
Anthropometric measures	
Body mass	0.8
Calf girth	0.5
Thigh girth	1.7
Upper arm girth	1.1

TABLE 10. Voluntary strength in control subjects (N = 24-25) measured as peak torque and power. Values are expressed absolutely and per kg body mass.

Movement			Peak torque		Peak power	
			N.m	N.m/kg	W	W/kg
Ankle plantar flexion						
	6 deg/s	left	240.4±52.0 (155.0-370.0)	3.37±0.70 (1.82-4.67)	25.2±5.4 (16.2-38.7)	0.353±0.073 (0.191-0.489)
		right	245.4±49.8 (165.0-355.0)	3.44±0.66 (2.21-5.03)	25.7±5.2 (17.3-37.2)	0.360±0.069 (0.231-0.527)
	36 deg/s	left	126.5±37.3 (60.0-200.0)	1.78±0.51 (0.71-2.51)	79.5±23.4 (37.7-125.6)	1.12±0.32 (0.45-1.58)
		right	132.7±37.1 (75.0-220.0)	1.85±0.46 (1.01-2.76)	83.4±23.3 (47.1-138.2)	1.16±0.29 (0.63-1.73)
Knee extension						
	30 deg/s	left	185.8±26.5 (115.0-240.0)	2.63±0.44 (1.70-3.33)	97.3±13.9 (60.2-125.6)	1.38±0.23 (0.89-1.74)
		right	202.5±35.9 (140.0-285.0)	2.84±0.53 (2.07-3.94)	106.0±18.8 (73.3-149.2)	1.49±0.28 (1.08-2/06)
	180 deg/s	left	144.1±25.6 (107.5-220.0)	2.03±0.37 (1.36-3.02)	452.6±80.4 (337.7-691.0)	6.38±1.16 (4.27-9.49)
		right	156.6±24.6 (120.0-225.0)	2.19±0.31 (1.65-3.09)	491.9±73.3 (376.9-706.7)	6.88±0.97 (5.18-9.71)

TABLE 10. Continued.

Elbow extension 30 deg/s	left	49.6±9.4 (30.0-67.5)	0.692±0.114 (0.510-0.880)	26.0±4.9 (15.7-35.3)	0.362±0.060 (0.267-0.461)
	right	53.0±12.6 (32.5-85.0)	0.736±0.141 (0.540-1.01)	27.7±6.6 (17.0-44.5)	0.385±0.074 (0.283-0.529)
180 deg/s	left	38.4±6.3 (22.5-50.0)	0.539±0.073 (0.390-0.650)	120.6±19.8 (70.7-157-1)	1.69±0.23 (1.22-2.04)
	right	43.9±13.0 (28.8-92.5)	0.603±0.149 (0.430-1.090)	137.9±40.8 (90.5-290.5)	1.89±0.47 (1.35-3.42)

Values are $\bar{x}$±SD/(min.-max.)

TABLE 11. Voluntary strength in control subjects (N = 24-25) measured as average torque and power. Values are expressed absolutely and per kg body mass.

Movement			Average torque		Average power	
			N.m	N.m/kg	W	W/kg
Ankle plantar flexion						
	6 deg/s	left	144.3±39.5 (83.2-237.3)	2.02±0.53 (1.12-3.36)	15.1±4.1 (8.7-24.9)	0.211±0.055 (0.117-0.352)
		right	142.4±36.5 (83.3-221.2)	1.98±0.44 (1.12-3.13)	14.9±3.8 (8.7-23.2)	0.207±0.046 (0.117-0.328)
	36 deg/s	left	71.5±19.9 (40.4-117.5)	1.00±0.27 (0.51-1.48)	44.9±12.5 (25.4-73.8)	0.628±0.170 (0.320-0.930)
		right	73.7±21.7 (39.4-130.0)	1.03±0.28 (0.53-1.63)	46.3±13.6 (24.8-81.7)	0.647±0.176 (0.333-1.024)
Knee extension						
	30 deg/s	left	107.8±20.1 (67.6-153.8	1.52±0.30 (0.95-2.11)	56.4±10.5 (35.4-80.5)	0.796±0.157 (0.497-1.105)
		right	118.0±25.2 (74.0-170.2)	1.66±0.41 (1.06-2.91)	61.8±13.2 (38.7-89.1)	0.869±0.215 (0.555-1.523)
	180 deg/s	left	72.5±16.1 (32.3-109.8)	1.02±0.24 (0.48-1.51)	227.7±50.6 (101.5-344.9)	3.20±0.75 (1.51-4.74)
		right	77.9±15.0 (48.3-116.3)	1.09±0.20 (0.71-1.60)	244.7±47.1 (151.7-365.3)	3.42±0.63 (2.23-5.03)

TABLE 11. Continued

Elbow extension 30 deg/s	left	39.0±8.6 (23.5-54.7)	0.545±0.115 (0.320-0.780)	20.4±4.5 (12.3-28.6)	0.285±0.060 (0.168-0.408)
	right	39.1±8.8 (19.2-54.4)	0.547±0.116 (0.230-0.810)	20.5±4.6 (10.1-28.5)	0.286±0.061 (0.120-0.424)
180 deg/s	left	28.9±5.1 (18.8-37.9)	0.404±0.066 (0.260-0.530)	90.8±16.0 (59.1-119.0)	1.27±0.21 (0.82-1.66)
	right	30.7±5.3 (21.6-44.1)	0.435±0.066 (0.320-0.680)	96.4±16.7 (67.9-138.5)	1.37±0.21 (1.01-2.14)

Values are $\bar{x}$±SD/(min.-max.)

TABLE 12. Voluntary strength in control subjects (N = 24-25) measured as impulse and work. Values are expressed absolutely and per kg body mass.

Movement		Impulse		Work	
		N.m.s	N.m.s/kg	J	J/kg
Ankle plantar flexion					
6 deg/s	left	236±84.3 (101.2-436.0)	3.31±1.11 (1.19-5.48)	24.8±8.8 (10.6-45.7)	0.347±0.116 (0.125-0.574)
	right	251.1±76.2 (136.0-420.0)	3.52±1.03 (1.96-5.28)	26.3±8.0 (14.2-44.0)	0.369±0.108 (0.205-0.533)
36 deg/s	left	32.2±12.7 (14.8-64.6)	0.450±0.172 (0.170-0.810)	20.2±8.0 (9.3-40.6)	0.283±0.108 (0.107-0.508)
	right	35.1±13.8 (11.4-58.6)	0.491±0.186 (0.180-0.770)	22.1±8.7 (7.2-36.8)	0.308±0.117 (0.107-0.484)
Knee extension					
30 deg/s	left	289.8±65.0 (164.0-408.0)	4.10±1.01 (2.43-6.26)	151.7±34.0 (85.9-213.6)	2.15±0.53 (1.27-3.28)
	right	317.4±77.3 (155.0-484.0)	4.45±1.11 (2.72-6.60)	166.2±40.5 (81.1-253.4)	2.33±0.58 (1.42-3.46)
180 deg/s	left	34.9±8.2 (19.4-49.4)	0.491±0.116 (0.270-0.730)	109.6±25.8 (60.9-155.2)	1.54±0.36 (0.85-2.29)
	right	39.2±7.7 (21.7-53.4)	0.547±0.110 (0.350-0.810)	123.1±24.2 (68.2-167.7)	1.72±0.35 (1.10-2.54)

TABLE 12. Continued.

Elbow extension 30 deg/s	left	148.6±28.7 (99.0-192.0)	2.08±0.39 (1.41-2.94)	77.8±15.0 (51.8-100.5)	1.09±0.20 (0.74-1.54)
	right	151.9±30.9 (100.0-200.0)	2.12±0.39 (1.22-2.75)	79.5±16.2 (52.4-104.7)	1.11±0.20 (0.64-1.44)
180 deg/s	left	19.7±3.0 (13.4-24.5)	0.278±0.037 (0.180-0.340)	61.9±9.4 (42.1-77.0)	0.873±0.116 (0.565-1.068)
	right	21.3±4.4 (14.5-35.3)	0.302±0.046 (0.220-0.420)	66.9±13.8 (45.6-110.9)	0.949±0.145 (0.691-1.319)

Values are $\bar{x}$±SD/(min.-max.)

TABLE 13. Correlations among mechanical properties of voluntary strength measurements in control subjects (N = 24-25)

Movement			Peak torque and power vs average torque and power	Peak torque and power vs impulse and work	Average torque and power vs impulse and work
Ankle plantar flexion	6 deg/s	left	0.90***	0.86***	0.70***
		right	0.90***	0.72***	0.62***
	36 deg/s	left	0.90***	0.88***	0.94***
		right	0.91***	0.89***	0.86***
Knee extension	30 deg/s	left	0.73***	0.59**	0.78***
		right	0.86***	0.75***	0.77***
	180 deg/s	left	0.74***	0.59**	0.85***
		right	0.68***	0.52**	0.87***
Elbow extension	30 deg/s	left	0.90***	0.87***	0.91***
		right	0.47*	0.61***	0.90***
	180 deg/s	left	0.80***	0.71***	0.78***
		right	0.66***	0.82***	0.78***

* p<0.02, ** p<0.01, *** p<0.001

The correlation coefficients ranged from r = 0.47 (elbow extension, 30 deg/s, right side, peak torque and power vs average torque and power) to r = 0.94 (ankle plantar flexion, 36 deg/s, left side, average torque and power vs impulse and work). The average correlation was, for peak torque and power vs average torque and power, r = 0.79; for peak torque and power vs impulse and work, r = 0.73 and for average torque and power vs impulse and work, r = 0.81. The correlations were not affected by the velocity or side of the body tested. The correlations among the mechanical properties were greater in ankle plantar flexion (r = 0.84) than in knee extension (r = 0.73) or elbow extension (r = 0.77).

The correlations among the three movements (ankle plantar flexion, knee extension and elbow extension) were generally low and non-significant. Of 36 possible correlations, only four were statistically significant (see Table 14). In each of the movements, however, the correlations between values for the left and right sides were in most cases positive and significant (see Table 15).

The results of the height, mass and limb girth measurements of the control subjects in the strength study are presented in Table 16. The correlations between these anthropometric measurements and the strength measurements are shown in Tables 17 - 19. In ankle plantar flexion (Table 17), the correlations were generally non-significant; only four of 48 possible correlations were significant. The significant correlations were low (r = 0.47 - 0.52). In knee extension (Table 18) the results were similar, with only one of 48 possible correlations being significant. In elbow extension, (Table 19), the correlation between

TABLE 14. Correlations among ankle plantar flexion, knee extension and elbow extension in the mechanical properties of voluntary strength measurements in control subjects ($N = 24\text{-}25$)

		Ankle plantar flexion vs Knee extension	Ankle plantar flexion vs Elbow extension	Knee extension vs Elbow extension
Peak torque and power				
low velocity	left	0.15	0.18	0.27
	right	0.10	0.23	0.30
high velocity	left	0.03	-0.13	-0.13
	right	0.30	0.13	0.29
Average torque and power				
low velocity	left	-0.03	0.05	0.68**
	right	0.11	0.13	0.27
high velocity	left	0.17	-0.10	0.38
	right	0.13	-0.02	0.37
Impulse and work				
low velocity	left	0.09	0.17	0.63**
	right	0.07	0.11	0.51*
high velocity	left	0.20	-0.14	0.60*
	right	-0.00	0.04	0.38

* $p<0.01$, ** $p<0.001$

Note: For elbow extension and knee extension, the low and high velocities were 30 deg/s and 180 deg/s respectively. For ankle plantar flexion, the low and high velocities were 6 deg/s and 36 deg/s respectively.

TABLE 15. Correlation between right and left sides in measurements of voluntary strength in control subjects (N = 24-25)

Movement		Left vs Right		
		Peak torque and power	Average torque and power	Impulse and work
Ankle plantar flexion	6 deg/s	0.69**	0.73**	0.65**
	36 deg/s	0.64**	0.66**	0.59**
Knee extension	30 deg/s	0.63**	0.63**	0.80**
	180 deg/s	0.75**	0.92**	0.95**
Elbow extension	30 deg/s	0.51*	0.80**	0.59*
	180 deg/s	0.37	0.62**	0.60**

*<p 0.01, ** p<0.001

TABLE 16. Height, body mass and limb girth measurements of the subjects used for the control voluntary strength measurements (N = 25).

Measure	$\bar{x}$	SD	Range
Height, cm	177.5	5.4	167.6 - 188.0
Body mass, kg	71.7	7.5	57.0 - 85.0
Calf girth, cm			
left	37.2	1.8	33.5 - 40.7
right	37.3	1.9	34.5 - 41.0
Thigh girth, cm			
left	55.6	2.4	50.4 - 59.5
right	56.0	2.7	50.6 - 61.0
Upper arm girth, cm			
left	30.2	1.5	27.0 - 33.3
right	30.2	1.5	27.0 - 33.6

TABLE 17. Correlations between ankle plantar flexion strength and height, mass and calf girth in control subjects (N = 18-25).

Measure			Height	Mass	Calf girth Left	Calf girth Right
Peak torque and power	6 deg/s	left	0.08	0.18	0.11	0.06
		right	0.05	0.31	0.35	0.30
	36 deg/s	left	0.14	0.07	0.04	-0.01
		right	0.19	0.39	0.51*	0.49*
Average torque and power	6 deg/s	left	0.13	0.22	0.04	-0.01
		right	0.26	0.48**	0.49*	0.45
	36 deg/s	left	0.03	0.13	0.11	0.08
		right	0.11	0.35	0.52*	0.47*
Impulse and work	6 deg/s	left	0.12	0.16	0.17	0.09
		right	0.16	0.27	0.30	0.28
	36 deg/s	left	0.06	0.09	0.14	0.08
		right	0.11	0.18	0.31	0.28

* $p<0.05$, ** $p<0.02$

TABLE 18. Correlations between knee extension strength and height, mass and thigh girth in control subjects (N = 18-25).

Measure			Height	Mass	Thigh girth	
					Left	Right
Peak torque and power	30 deg/s	left	-0.07	0.09	0.16	0.07
		right	0.36	0.23	-0.00	-0.06
	180 deg/s	left	0.26	0.23	0.12	0.02
		right	0.33	0.41*	0.07	0.03
Average torque and power	30 deg/s	left	0.00	0.10	0.03	-0.00
		right	0.20	0.06	0.08	0.07
	180 deg/s	left	0.13	0.14	0.11	0.07
		right	0.30	0.33	0.08	0.04
Impulse and work	30 deg/s	left	0.02	0.08	-0.16	-0.17
		right	0.20	0.26	-0.07	-0.01
	180 deg/s	left	0.12	0.20	0.03	0.02
		right	0.18	0.25	-0.10	-0.09

* $p<0.05$

TABLE 19. Correlations between elbow extension strength and height, mass and upper arm girth in control subjects (N = 19-25).

Measure			Height	Mass	Upper arm girth	
					Left	Right
Peak torque and power	30 deg/s	left	0.16	0.47	0.64	0.66***
		right	0.50**	0.62****	0.19	0.20
	180 deg/s	left	0.20	0.58***	0.48*	0.55**
		right	0.31	0.56***	0.15	0.14
Average torque and power	30 deg/s	left	0.07	0.28	0.50*	0.52*
		right	0.16	0.26	0.28	0.41
	180 deg/s	left	0.10	0.40*	0.52*	0.50*
		right	0.28	0.41*	0.21	0.32
Impulse and work	30 deg/s	left	0.12	0.31	0.47*	0.46*
		right	0.31	0.37	0.20	0.37
	180 deg/s	left	0.10	0.46**	0.57***	0.63***
		right	0.31	0.48**	0.04	0.17

* $p<0.05$, ** $p<0.02$, *** $p<0.01$, **** $p<0.001$

strength and the anthropometric measurements was greater; 20 of 48 possible correlations were significant. However, the significant correlations were again low (r = 0.46 - 0.66).

There was a significant, positive correlation between low and high velocity strength performance (Table 20). The correlations ranged from r = 0.44 to r = 0.84 ($\bar{x}$:r = 0.74). The correlations did not vary in relation to the movement, mechanical property and side tested, except in the case of peak torque and power in knee extension, where the correlation was notably lower.

The results of the strength-velocity relation determinations are presented in Table 21. The following average strength-velocity relation ratios were obtained when the values for the three movements and right and left sides were combined: peak power, 4.26; average power, 3.94; work, 0.804; peak torque, 0.710; average torque, 0.656 and impulse, 0.134. It should be noted that peak and average power increased when tested at the high velocity, whereas the remaining properties decreased at the high velocity. The results were similar for left and right sides.

It was not possible to compare the strength-velocity relation ratios of ankle plantar flexion with those of knee extension and elbow extension because of differences in the testing procedures (see Methods); however, similar testing procedures made it possible to compare knee extension with elbow extension in this respect. The results are shown in Table 22. In peak torque and power, there was no difference between elbow extension and knee extension in the strength-velocity relation; however, the values for elbow extension exceeded those of knee

TABLE 20. Correlation between low and high velocity values of mechanical properties of voluntary strength measurements in control subjects. (N = 24-25).

Movement		Peak torque and power	Average torque and power	Impulse and work
Ankle plantar flexion 6 deg/s vs 36 deg/s	left	0.74***	0.79***	0.72***
	right	0.71***	0.83***	0.80***
Knee extension 30 deg/s vs 180 deg/s	left	0.44*	0.80***	0.79***
	right	0.58**	0.71***	0.79***
Elbow extension 30 deg/s vs 180 deg/s	left	0.77***	0.78***	0.84***
	right	0.77***	0.74***	0.65***

* $p<0.05$, ** $p<0.005$, *** $p<0.001$

TABLE 21. Strength-velocity relation (value at high velocity/value at low velocity) in control subjects (N = 24-25).

Movement	Strength-velocity relation					
	Peak torque	Peak power	Average torque	Average power	Impulse	Work
Ankle plantar flexion (36 deg/s)/ (6 deg/s) left	0.533±0.106	3.20±0.64	0.505±0.100	3.03±0.60	0.140±0.038	0.840±0.228
	(0.300-0.800)	(1.80-4.80)	(0.310-0.770)	(1.86-4.62)	(0.060-0.230)	(0.360-1.380)
right	0.540±0.106	3.24±0.64	0.523±0.086	3.14±0.52	0.139±0.038	0.834±0.228
	(0.400-0.790)	(2.40-4.74)	(0.390-0.710)	(2.34-4.26)	(0.080-0.210)	(0.480-1.260)
Knee extension (180 deg/s)/ (30 deg/s) left	0.783±0.131	4.70±0.79	0.672±0.096	4.03±0.58	0.122±0.020	0.732±0.120
	(0.560-1.050)	(3.36-6.30)	(0.480-0.830)	(2.88-4.98)	(0.090-0.160)	(0.540-0.960)
right	0.786±0.122	4.72±0.73	0.672±0.103	4.03±0.62	0.126±0.021	0.756±0.126
	(0.530-1.030)	(3.18-6.18)	(0.430-0.890)	(2.58-5.34)	(0.100-0.180)	(0.600-1.080)

TABLE 21. Continued.

Elbow extension (180 deg/s)/ 30 deg/s)						
left	0.783±0.090	4.70±0.54	0.755±0.104	4.53±0.62	0.135±0.016	0.810±0.096
	(0.590-0.940)	(3.54-5.64)	(0.610-1.060)	(3.66-6.36)	(0.110-0.180)	(0.660-1.080)
right	0.833±0.142	5.00±0.85	0.807±0.147	4.84±0.88	0.142±0.024	0.852±0.144
	(0.630-1.140)	(3.78-6.84)	(0.630-1.260)	(3.78-7.56)	(0.110-0.200)	(0.660-1.200)

Values are $\bar{x}$±SD/(min.-max.)

TABLE 22 Comparison of strength-velocity relation ratios of knee extension with those of elbow extension in control subjects (N = 24-25).

Mechanical property		Strength-velocity relation ratio		
		Knee extension	Elbow extension	Difference
Peak torque	left	0.783±0.027	0.783±0.018	0.000±0.036
	right	0.786±0.024	0.833±0.028	0.047±0.040
Peak power	left	4.70±0.16	4.70±0.11	0.00±0.22
	right	4.72±0.14	5.00±0.17	0.28±0.24
Average torque	left	0.672±0.020	0.755±0.021	0.083±0.026***
	right	0.672±0.021	0.807±0.029	0.135±0.039***
Average power	left	4.03±0.12	4.53±0.13	0.50±0.156***
	right	4.03±0.13	4.84±0.17	0.81±0.234***
Impulse	left	0.122±0.004	0.135±0.003	0.013±0.005**
	right	0.126±0.004	0.142±0.005	0.016±0.007*
Work	left	0.732±0.024	0.810±0.018	0.078±0.030**
	right	0.756±0.024	0.852±0.030	0.096±0.042*

Values are $\bar{x} \pm SE$

* $p<0.05$, ** $p<0.025$, *** $p<0.005$

extension by 16% in average torque and power and by 12% in impulse and work.

The correlations among the mechanical properties in the strength-velocity relation are shown in Table 23. The correlations were generally positive and significant. The average correlation between peak torque and power and impulse and work was slightly higher (r = 0.63) than the correlation between peak torque and power and average torque and power (r = 0.56) and the correlation between average torque and power and impulse and work (r = 0.54). There was some variation in the correlations in relation to the side (left, r = 0.52 ; right, r = 0.63) and the movement (ankle plantar flexion, r = 0.63; knee extension, r = 0.56; elbow extension, r = 0.54) tested.

There were no significant correlations among the three movements tested in the strength-velocity relation ratios.

The correlations between the strength-velocity relation ratios and the mechanical properties for ankle plantar flexion, knee extension and elbow extension are presented in Tables 24-26 respectively. All of the significant positive correlations were between the strength-velocity relation ratios and the mechanical properties measured at high velocity, while all of the significant negative correlations were between the strength-velocity relation ratios and the mechanical properties measured at low velocity.

The symmetry ratios of the voluntary strength measurements are presented in Table 27. The overall symmetry ratio was 0.865. There was a small variation in relation to the mechanical property (peak torque and power, 0.867; average torque and power, 0.877; impulse and work,

TABLE 23. Correlations among the mechanical properties of voluntary strength measurements in control subjects (N = 24-25) when expressed as strength-velocity relation ratios.

Movement		Peak torque and power vs average torque and power	Peak torque and power vs impulse and work	Average torque and power vs impulse and work
Ankle plantar flexion	left	0.70***	0.67***	0.44*
	right	0.69***	0.66***	0.62***
Knee extension	left	0.39	0.48*	0.67***
	right	0.66***	0.63***	0.54**
Elbow extension	left	0.50*	0.55**	0.28
	right	0.44*	0.76***	0.68***

* p<0.05, ** p<0.01, *** p<0.001

TABLE 24. Correlation between strength-velocity relation ratios and mechanical properties in ankle plantar flexion (N = 24-25).

Mechanical property			Strength-velocity relation ratio		
			Peak torque and power	Average torque and power	Impulse and work
Peak torque and power	6 deg/s	left	0.00	-0.13	0.05
		right	-0.00	-0.01	0.30
	36 deg/s	left	0.62****	0.34	0.48**
		right	0.69****	0.46**	0.66****
Average torque and power	6 deg/s	left	-0.01	-0.29	0.19
		right	0.10	-0.12	0.28
	36 deg/s	left	0.41*	0.35	0.48**
		right	0.48**	0.44*	0.57***
Impulse and work	6 deg/s	left	0.08	-0.08	-0.22
		right	0.12	0.14	0.08
	36 deg/s	left	0.42*	0.32	0.49**
		right	0.51***	0.48**	0.63****

* p<0.05, ** p<0.02, *** p<0.01, **** p<0.001

TABLE 25. Correlation between strength-velocity relation ratios and mechanical properties in knee extension (N = 24-25).

Mechanical property			Strength-velocity relation ratio		
			Peak torque and power	Average torque and power	Impulse and work
Peak torque and power	30 deg/s	left	-0.41*	0.10	0.14
		right	-0.61****	-0.33	-0.44*
	180 deg/s	left	0.62****	0.53***	0.60***
		right	0.29	0.28	0.10
Average torque and power	30 deg/s	left	-0.14	-0.10	0.03
		right	-0.67****	-0.50**	-0.50**
	180 deg/s	left	0.19	0.58***	0.45*
		right	-0.20	0.24	-0.12
Impulse and work	30 deg/s	left	-0.28	-0.07	-0.28
		right	-0.55***	-0.18	-0.62****
	180 deg/s	left	0.06	0.34	0.35
		right	-0.22	0.24	-0.03

* $p<0.05$, ** $p<0.02$, *** $p<0.01$, **** $p<0.001$

TABLE 26. Correlation between strength-velocity relation ratios and mechanical properties in elbow extension (N = 24-25).

Mechanical property			Strength-velocity relation ratio		
			Peak torque and power	Average torque and power	Impulse and work
Peak torque and power	30 deg/s	left	-0.50**	-0.35	-0.47**
		right	-0.15	0.12	-0.02
	180 deg/s	left	0.15	-0.12	-0.12
		right	0.50**	0.35	0.47**
Average torque and power	30 deg/s	left	-0.51***	-0.58***	-0.42*
		right	-0.25	-0.67****	-0.42*
	180 deg/s	left	-0.21	0.03	-0.24
		right	0.18	-0.05	0.12
Impulse and work	30 deg/s	left	-0.53***	-0.43*	-0.60****
		right	-0.26	-0.57***	-0.44*
	180 deg/s	left	-0.28	-0.32	-0.09
		right	0.39	-0.01	0.39

* $p<0.05$, ** $p<0.02$, *** $p<0.01$, **** $p<0.001$

TABLE 27 Symmetry ratios (value for weaker side/value for stronger side) of the voluntary strength measurements in control subjects (N = 24-25)

Movement		Symmetry ratio		
		Peak torque and power	Average torque and power	Impulse and work
Ankle plantar flexion	6°/s	0.879±0.071 (0.70-1.00)	0.863±0.094 (0.58-1.00)	0.806±0.101 (0.66-0.99)
	36°/s	0.830±0.144 (0.45-1.00)	0.838±0.121 (0.46-0.97)	0.776±0.174 (0.35-0.98)
Knee extension	30°/s	0.885±0.84 (0.68-1.00)	0.880±0.104 (0.59-1.00)	0.890±0.090 (0.64-0.99)
	180°/s	0.888±0.078 (0.77-1.00)	0.905±0.070 (0.67-1.00)	0.890±0.075 (0.67-1.00)
Elbow extension	30°/s	0.878±0.108 (0.52-1.00)	0.885±0.068 0.71-1.00)	0.864±0.086 (0.67-1.00)
	180°/s	0.842±0.128 (0.45-1.00)	0.892±0.94 (0.68-1.00)	0.889±0.098 (o.64-1.00)

Values are mean ± SD/(min.-max.)

0.853) the movement (ankle plantar flexion, 0.830; knee extension, 0.890; elbow extension, 0.875) and the velocity (slow, 0.870; fast 0.861) tested.

2. Motor Unit Counts. The results of the motor unit counting measurements are presented in Table 28. In 20 subjects (brachioradialis, N = 4; extensor digitorum brevis, N = 8; hypothenar, N = 1; soleus, N = 2; thenar, N = 5), motor unit counts were made on both left and right sides. On the average, the values for the right side exceeded those for the left side by 7%, but this difference was not significant. The correlation between the values for the left and right sides was r = 0.78 ($p<0.001$). The mean (±SD) symmetry ratio was 0.67±0.21.

In these same subjects, the corresponding comparisons were made in the M-wave measurements. On the average, the values for the right side exceeded those for the left side by 12%, but this difference was not significant. The correlation between the values for the left and right sides was r = 0.88 ($p<0.001$). The mean (±SD) symmetry ratio was 0.75±0.22.

3. Motor Nerve Conduction Velocity. The results of the motor nerve conduction velocity measurements are presented in Table 29. The values for the ulnar and median nerves were similar, and were approximately 26% greater than the value for the deep peroneal nerve.

In 12 subjects (deep peroneal nerve, N = 8; median nerve, N = 3; ulnar nerve, N = 1), measurements were made on both left and right sides. There was no difference between the values for the two sides. The correlation between the values for the left and right sides was r = 0.81 ($p<0.01$). The mean (±SD) symmetry ratio was 0.95±0.04.

TABLE 28. Motor unit counts, mean motor unit potential amplitude and M waves in control subjects.

Muscle	N	Number of motor units	Mean motor unit potential amplitude (uV)	M-wave (mV)
Brachioradialis	48	864±546 (270-1428)	12.3±3.4 (6.2-24.1)	9.4±3.5 (3.4-20.0)
Extensor digitorum brevis	25	200±88 (77-444)	44.6±20.2 (12.0-100.0)	8.5±3.3 (3.8-19.0)
Hypothenar	14	504±128 (308-820)	29.0±9.2 (17.5-50.0)	13.9±3.0 (10.6-19.5)
Soleus	43	1045±499 (324-3520)	27.2±12.2 (7.2-74.4)	24.3±6.0 (12.5-38.5)
Thenar	26	304±157 (79-760)	38.4±20.6 (15.0-122.0)	9.7±2.7 (5.6-14.6)

Values are $\bar{x}$±SD/(min-max)

TABLE 29. Motor nerve conduction velocities in control subjects.

Nerve	N	Motor nerve conduction velocity, m/s		
		$\bar{x}$	SD	Range
Deep peroneal	24	47.5	3.1	42-53
Median	31	58.9	3.2	53-67
Ulnar	13	60.2	4.9	48-67

In 11 subjects, the correlation between the values for the ulnar and median nerves was $r = 0.73$ ($p<0.02$). In 11 subjects, the correlation between the values for the median and deep peroneal nerve was $r = 0.64$ ($p<0.05$).

4. Reflex Potentiation. The results of the reflex potentiation measurements are presented in Figures 10-12 and Table 30. The values for both V_1 and V_2 potentiation were greatest in thenar and brachioradialis muscles. The correlation between the V_1 and V_2 values was, for the thenar muscles, $r = 0.63$ ($p<0.001$); hypothenar muscles, $r = 0.58$ ($p<0.05$); brachioradialis, $r = 0.63$ ($p<0.001$) and extensor digitorum brevis, $r = 0.86$ ($p<0.001$).

In 10 subjects (extensor digitorum brevis, $N = 6$; brachioradialis, $N = 2$; thenar, $N = 2$), measurements were made on both left and right sides. For both V_1 and V_2 potentiation, there was no significant difference between the values for the left and right sides. The correlation between the left and right sides was, for V_1, $r = 0.67$ ($p<0.05$) and for V_2, $r = 0.77$ ($p<0.01$). The mean (±SD) symmetry ratio was, for V_1, 0.63 ± 0.23 and for V_2, 0.69 ± 0.17.

There was little correlation among muscles in reflex potentiation (see Table 31). An exception was a significant positive correlation between thenar V_2 and hypothenar V_2 potentiation ($r = 0.66$, $p<0.05$).

5. Muscle Twitch Properties. The results of the measurement of the muscle twitch properties are shown in Figures 13-16 and in Table 32.

The correlations among the twitch properties are presented in Table 33. Significant positive correlations were found between twitch

Figure 10. Reflex potentiation in the median innervated thenar muscles. A-D: responses in four subjects at rest and during maximal isometric contraction (effort). 10 ms time marks.

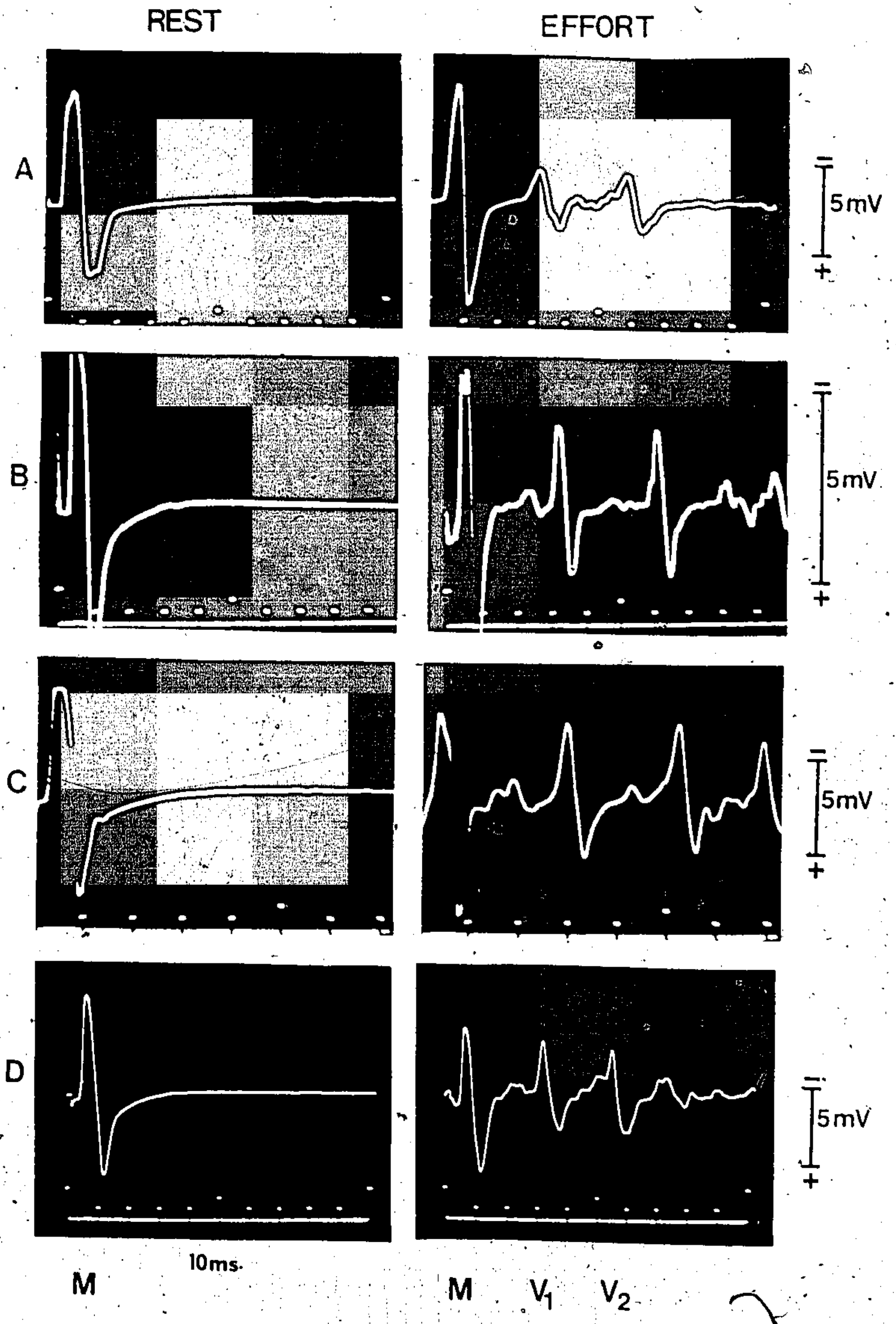

REST
EFFORT
A
B
C
D
5mV
5mV
5mV
5mV
+
+
+
+
10ms.
M
M
V1
V2

Figure 11. Reflex potentiation in brachioradialis (A), hypothenar (B) and extensor digitorum brevis (C) in three subjects. Responses at rest and during maximal isometric contractions (effort) are shown. 10 ms time marks.

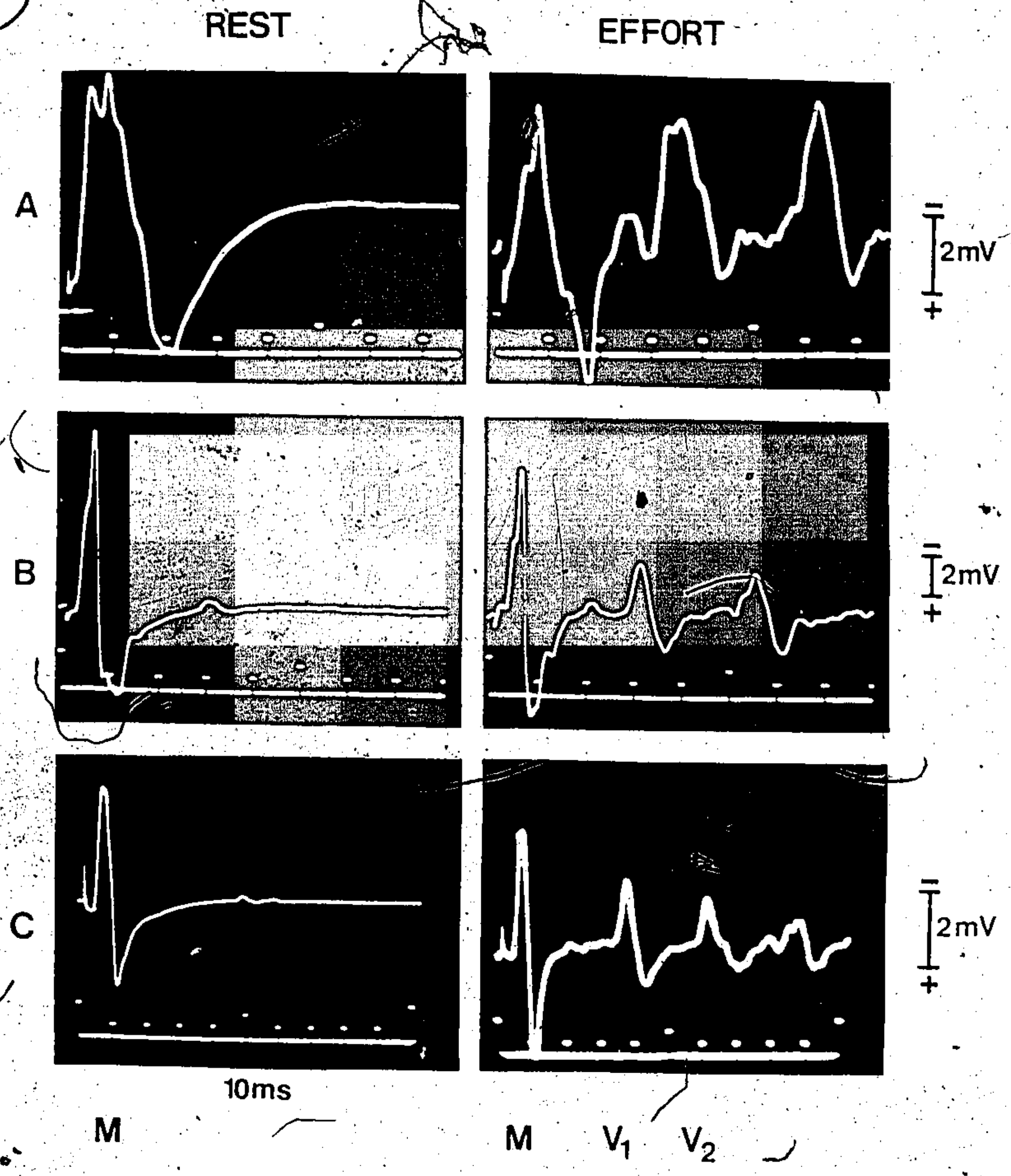

REST
EFFORT
A
B
C
2mV
2mV
2mV
+
+
+
10ms
M
M
V_1
V_2

Figure 12. Reflex potentiation in soleus. A-D: responses in four subjects at rest and during maximal isometric contraction (effort). 10 ms time marks.

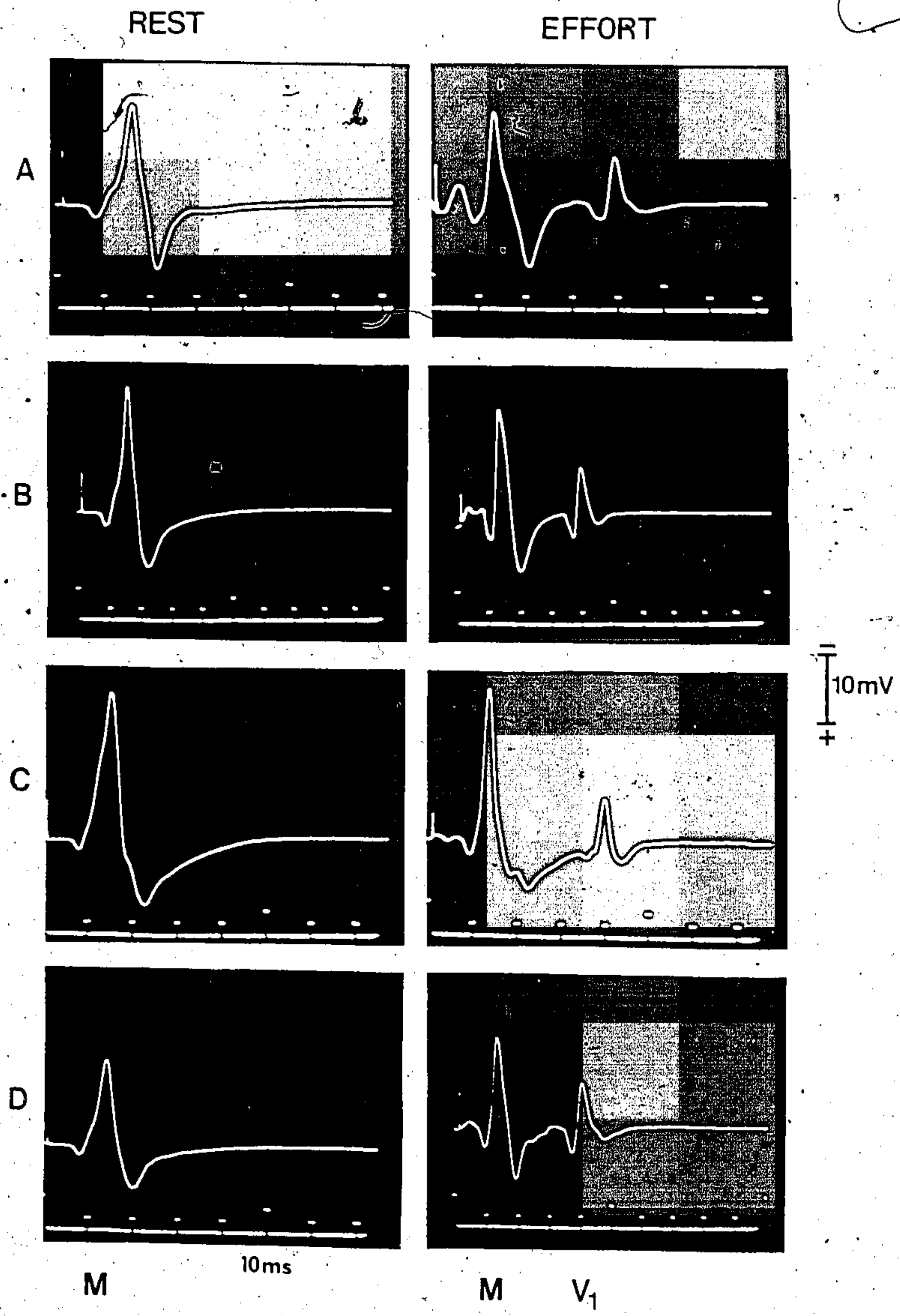

REST
EFFORT
A
B
C
D
10mV
10ms
M
M
V_1

TABLE 30. Reflex potentiation in control subjects

Muscle	N	Reflex potentiation	
		V1/Mx100, %	V2/Mx100, %
Thenar	28	27.6±13.4 (7-68)	24.1±12.4 (1-54)
Hypothenar	13	15.0±7.1 (5-32)	15.1±6.7 (4-27)
Brachioradialis	35	31.4±18.2 (4-67)	26.7±14.7* (3-54)
Soleus	29	15.3±9.3 (3-47)	**
Extensor digitorum brevis	16	11.1±7.4 (2-23)	18.1±9.3 (5-33)

Values are $\bar{X}$ ± SD/(min-max).

*For this measurement, N = 32.

**In soleus, this measurement was not made.

TABLE 31. Correlations among muscles in reflex potentiation in control subjects.

Measure		N	r	p
Thenar, V_1	vs soleus, V_1	13	-0.04	NS
Thenar, V_1	vs hypothenar, V_1	11	0.10	NS
Thenar, V_1	vs hypothenar, V_2	11	0.37	NS
Thenar, V_2	vs soleus, V_1	13	0.28	NS
Thenar, V_2	vs hypothenar, V_1	11	0.55	NS
Thenar, V_2	vs hypothenar, V_2	11	0.66	0.05
Soleus, V_1	vs hypothenar, V_1	12	0.13	NS
Soleus, V_1	vs hypothenar, V_2	12	0.02	NS
Brachioradialis, V_1	vs extensor digitorum brevis, V_1	7	0.50	NS
Brachioradialis, V_1	vs extensor digitorum brevis, V_2	7	0.73	NS
Brachioradialis, V_2	vs extensor digitorum brevis, V_1	7	0.66	NS
Brachioradialis, V_2	vs extensor digitorum brevis, V_2	7	0.61	NS

Figure 13. Muscle twitch recordings of triceps surae in eight different subjects. A: AS, male, 20y; B: RF, male, 20y; C: JS, male, 20y; D: SV, female, 20y; E: GC, male, 19y; F: BB, male, 21y; G: JB, male, 19y; H: CVB, female, 20y. 10 ms time marks.

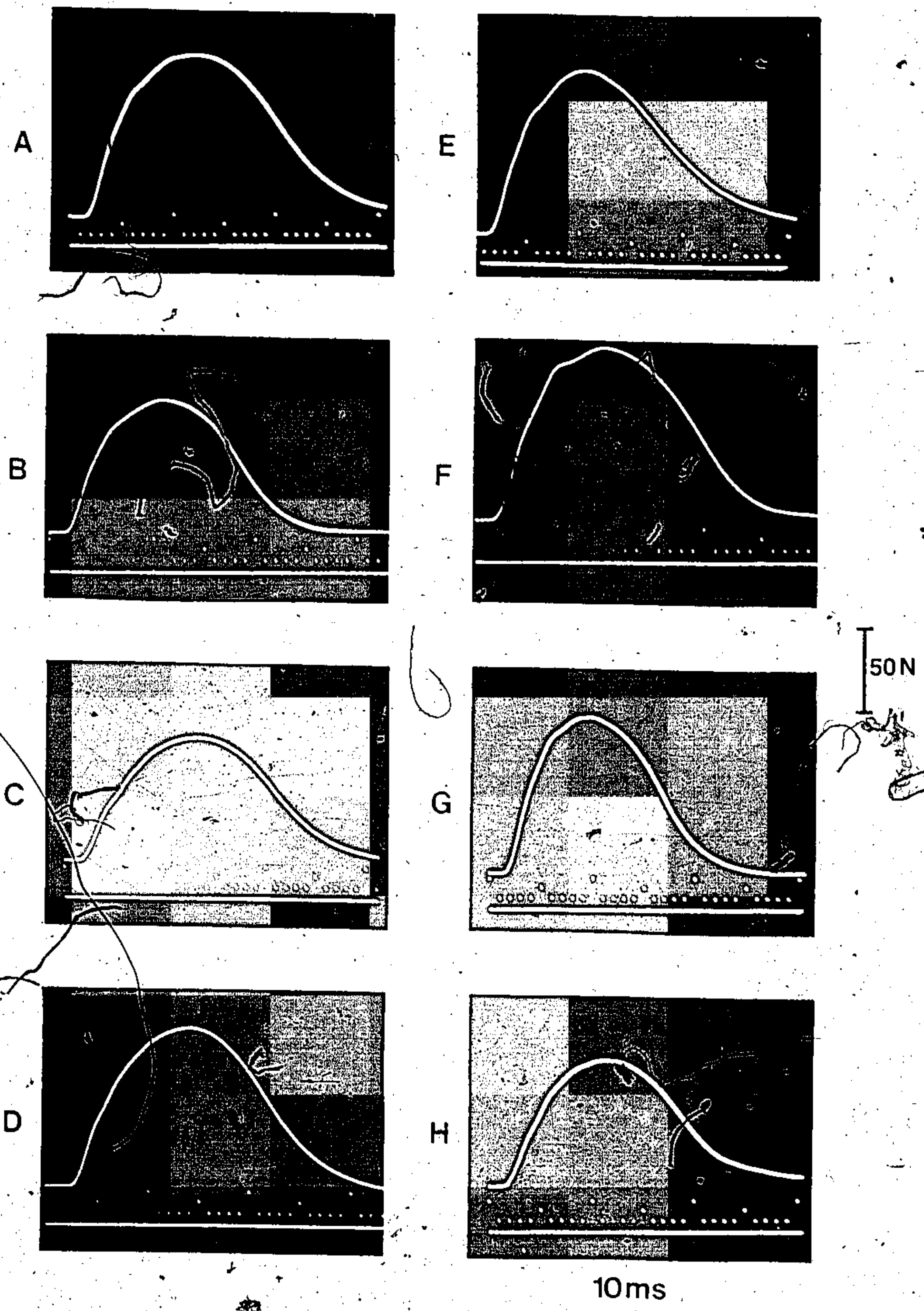

A
B
C
D
E
F
G
H
50N
10ms

Figure 14. Muscle twitch recordings of extensor hallucis brevis in eight different subjects. A: DH, male, 30y; B: JC, male, 27y; C: LS, female, 20y; D: PM, female, 19y; E: MP, male, 21y; F: CR, female, 21y; G: CW, male, 21y; H: AC, female, 20y. 10 ms time marks.

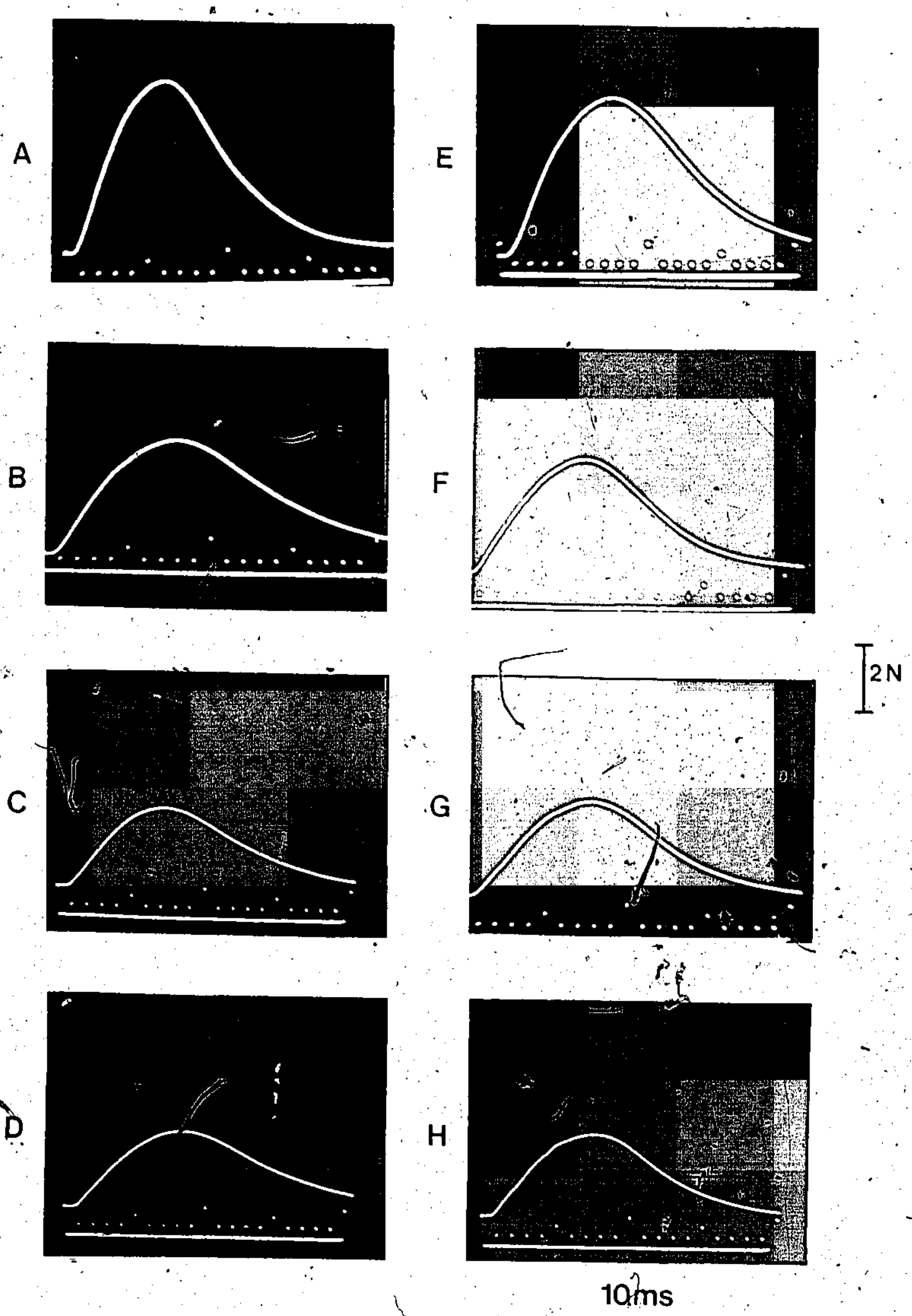

A
E
B
F
C
G
2N
D
H
10ms

Figure 15. Muscle twitch recordings of the hypothenar muscles in eight different male subjects. A: GS, 21y; B: CV, 20y; C: GC, 19y; D: WH, 20y; E: HS, 24y; F: AS, 21y; G: TT, 20y; H: DH, 30y. 10 ms time marks.

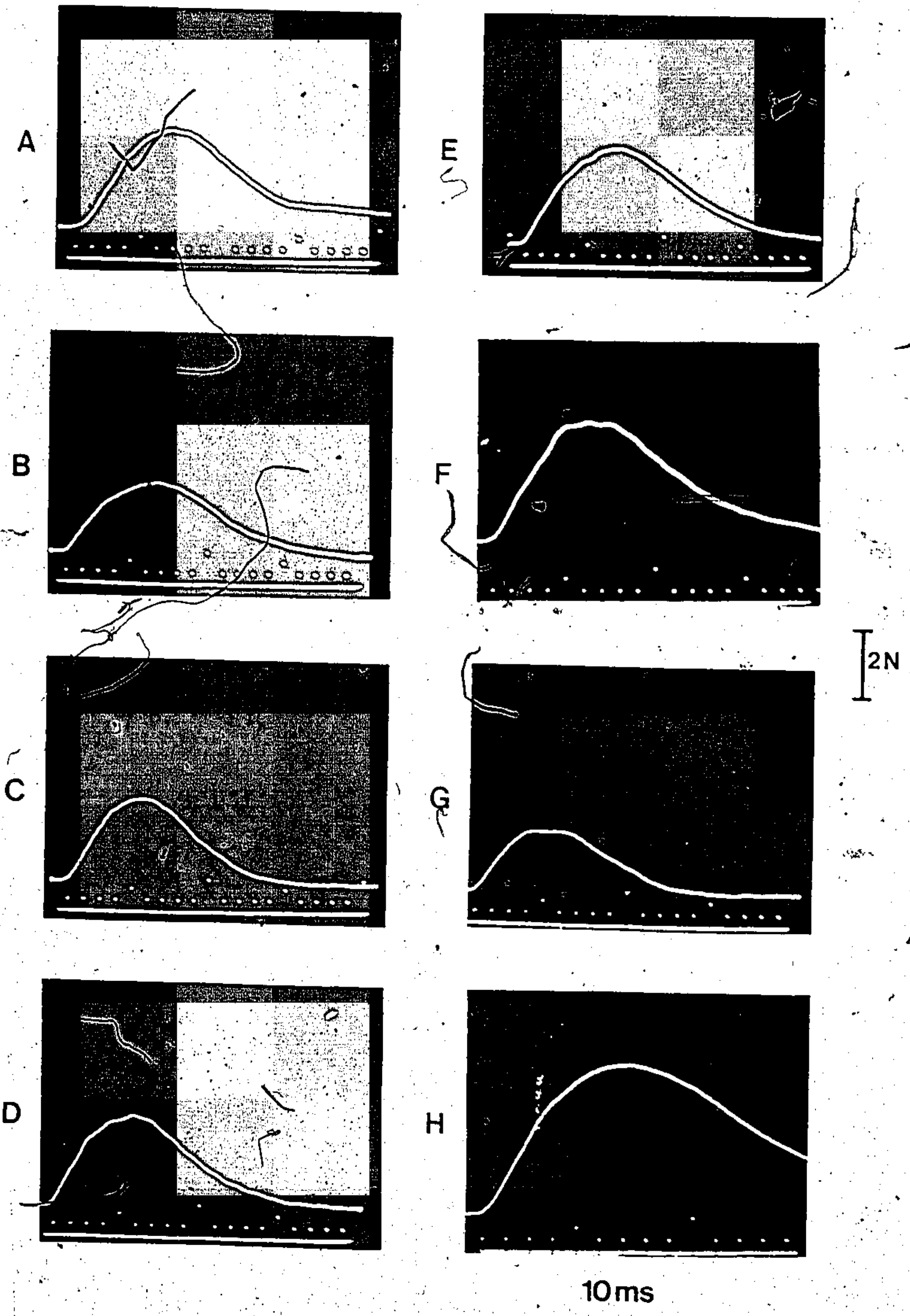

A
B
C
D
E
F
G
H
2N
10ms

Figure 16. Muscle twitch recordings of the median-innervated thenar muscles in eight different male subjects. A: HW, 25y; B: RN, 20y; C: RG, 19y; D: BD, 20y; E: GC, 19y; F: SW, 19y; G: CV, 20y; H: MC, 20y. 10 ms time marks.

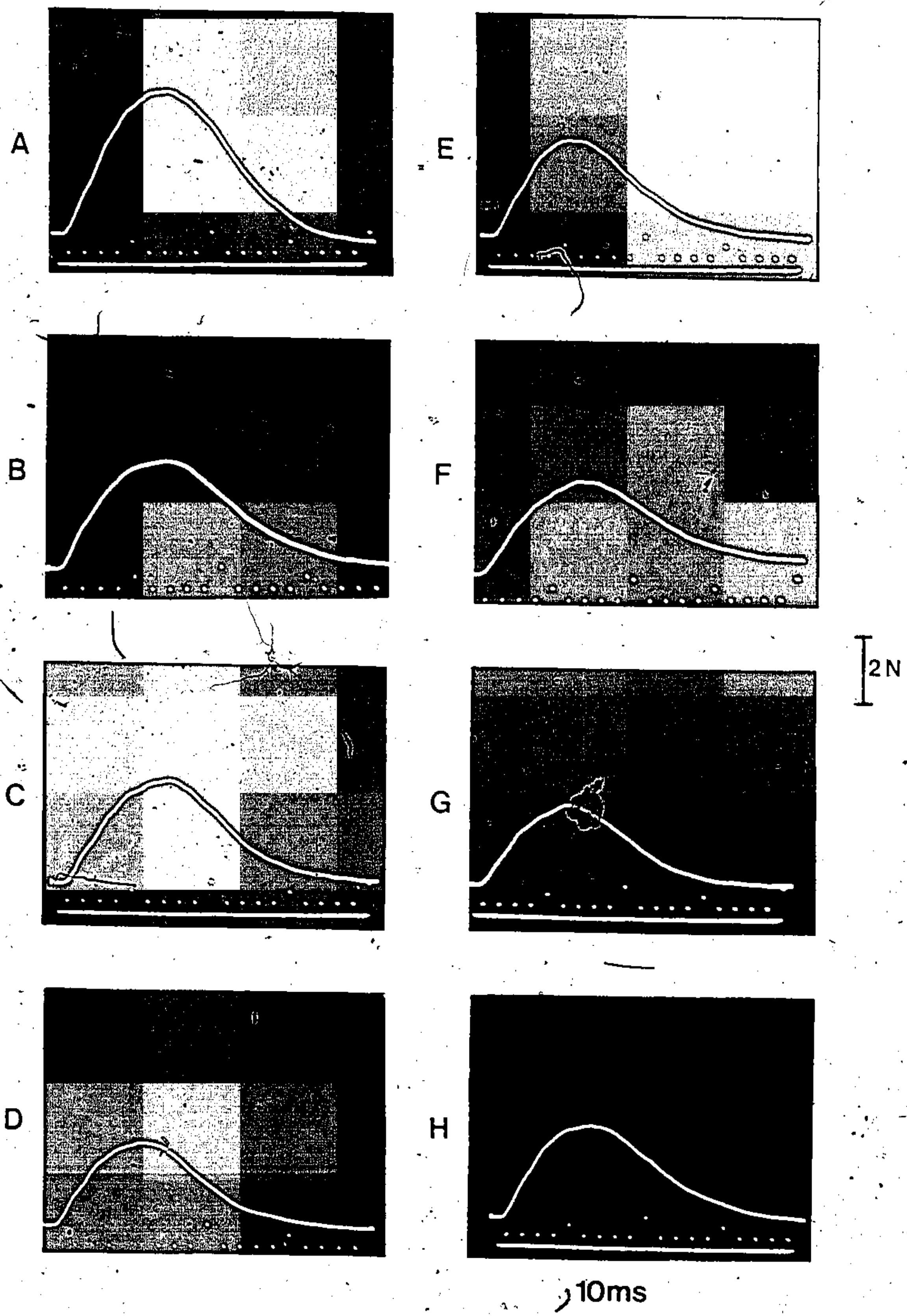

A
E
B
F
C
G
D
H
2N
10ms

TABLE 32. Muscle twitch properties in control subjects

Muscle	N	Twitch tension N	Contraction time ms	Rate of tension development N/s	Half relaxation time ms
Extensor hallucis brevis	5	2.17±0.34 (1.77-2.44)	73.2±10.3 (64-91)	29.7±3.8 (27.5-36.4)	62.4±7.4 (53-69)
Hypothenar	19	2.62±0.88 (1.31-4.61)	56.5±5.7 (47-67)	46.4±15.2 (23.4-88.7)	51.1±9.4 (37-62)
Thenar	19	2.33±0.74 (1.18-3.63)	53.4±7.2 (35-62)	45.1±17.7 (19.0-89.6)	49.8±8.0 (37-62)
Triceps surae	56	93.6± 18.0 (56.9-137.3)	106.4±14.1 (75-135)	887.5±177.8 (569.8-1380.8)	87.3±15.5 (58-118)

Values are $\bar{X}\pm SD$/(min-max)

TABLE 33. Correlations among twitch properties in control subjects.

Properties	Extensor hallucis brevis (N = 5)	Hypothenar (N = 19)	Thenar (N = 19)	Triceps surae (N = 56)
T vs CT	0.65	0.27	-0.26	0.31*
vs RTD	0.59	0.95***	0.15	0.74***
vs 1/2RT	-0.09	0.10	0.01	0.17
CT vs RTD	-0.22	-0.03	-0.65**	-0.39**
vs 1/2RT	0.52	0.12	0.17	0.16
RTD vs 1/2RT	-0.67	0.08	-0.00	0.07

T = twitch tension, CT = contraction time, RTD = rate of tension development, 1/2 RT = half relaxation time

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$

tension and rate of tension development (hypothenar, triceps surae). A significant negative correlation was found between contraction time and rate of tension development (thenar, triceps surae).

In 35 subjects, there was no correlation between the twitch tension of triceps surae and the M wave amplitude of soleus, nor was there any correlation between the soleus M wave amplitude and calf girth ($n = 19$). There was a low but significant correlation ($r = 0.35$, $p<0.05$) between twitch tension of triceps surae and calf girth ($N = 38$). In thenar ($N = 19$) and hypothenar ($N = 13$) muscles, there was no correlation between twitch tension and M wave amplitude.

There were no significant correlations among the muscles in any of the twitch properties.

In 12 subjects, the twitch properties of triceps surae and calf girth were measured on both left and right sides. The half relaxation time of the right side was 12% ($p<0.05$) longer than that of the left side. There were no significant differences in any of the other twitch properties, nor in calf girth. The correlation between left and right sides was, for twitch tension, $r = 0.93$ ($p<0.01$); contraction time, $r = 0.60$ ($p<0.05$); rate of tension development, $r = 0.90$ ($p<0.01$); half relaxation time, $r = 0.72$ ($p<0.01$) and for calf girth, $r = 0.99$ ($p<0.001$). The mean (±SD) symmetry ratio was, for twitch tension, 0.94 ± 0.04; contraction time, 0.94 ± 0.05; rate of tension development, 0.93 ± 0.07; half relaxation time, 0.86 ± 0.10 andfor calf girth, 0.99 ± 0.01.

A comparison of male and female control subjects in the twitch properties of triceps surae and in calf girth is presented in Table 34. Rate of tension development was greater by 13% and calf girth by 5% in

TABLE 34. Comparison of male and female control subjects in the twitch properties of the triceps surae muscle and in calf girth.

Property	Males (N = 46)	Females (N = 10)	Difference
Twitch tension, N	93.8±2.8	92.6±3.2	1.2±4.3
Contraction time, ms	104.4±2.1	115.8±3.7	11.4±4.2*
Rate of tension development, N/s	906.1±27.5	802.2±23.5	103±36.3**
Half relaxation time, ms	85.2±2.1	96.6±5.6	11.4±6.0
Calf girth, cm	36.4±0.4	34.6±0.6	1.8±0.7*

Values are $\bar{X} \pm$ SE

*$p < 0.02$, **$p < 0.01$

the males. Contraction time was 11% longer in the females.

C. Training and Immobilization Experiments.

1. Voluntary Strength. The results for subjects in which elbow extension strength was measured after both training and immobilization are presented in Figure 17. In the group which immobilized prior to training, peak torque decreased by 25% ($p<0.005$) after immobilization, and after training increased by 77% ($p<0.05$) over the post immobilization value and by 33% (NS) over the control value. Average torque decreased by 30% ($p<0.005$) after immobilization, and after training increased by 84% ($p<0.02$) over the post immobilization value and by 28% ($p<0.05$) over the control value. Impulse decreased by 39% (p 0.025) after immobilization, and after training increased by 115% ($p<0.05$) over the post immobilization value and by 31% (NS, $p<0.10$) over the control value.

In the group which trained prior to immobilization, peak torque increased by 50% (NS) after training, and after immobilization, decreased by 39% (NS, $p<0.10$) from the post training value and by 8% (NS) from the control value. Average torque increased by 24% ($p<0.05$) after training, and after immobilization, decreased by 30% ($p<0.001$) from the post training value and by 13% (NS) from the control value. Impulse increased by 12% (NS) after training, and after immobilization, decreased by 30% ($p<0.001$) from the post training value and by 22% (NS, $p<0.10$) from the control value.

When the results of those subjects who immobilized first were combined with the results of those who trained first, the overall results were as shown in Table 35. The post training value exceeded the control

Figure 17. Effect of training and immobilization upon elbow extension strength. Left: the group which immobilized prior to training; right: the group which trained prior to immobilization; C = control, I = after immobilization, T = after training. Values are $\bar{X}$ and SE.

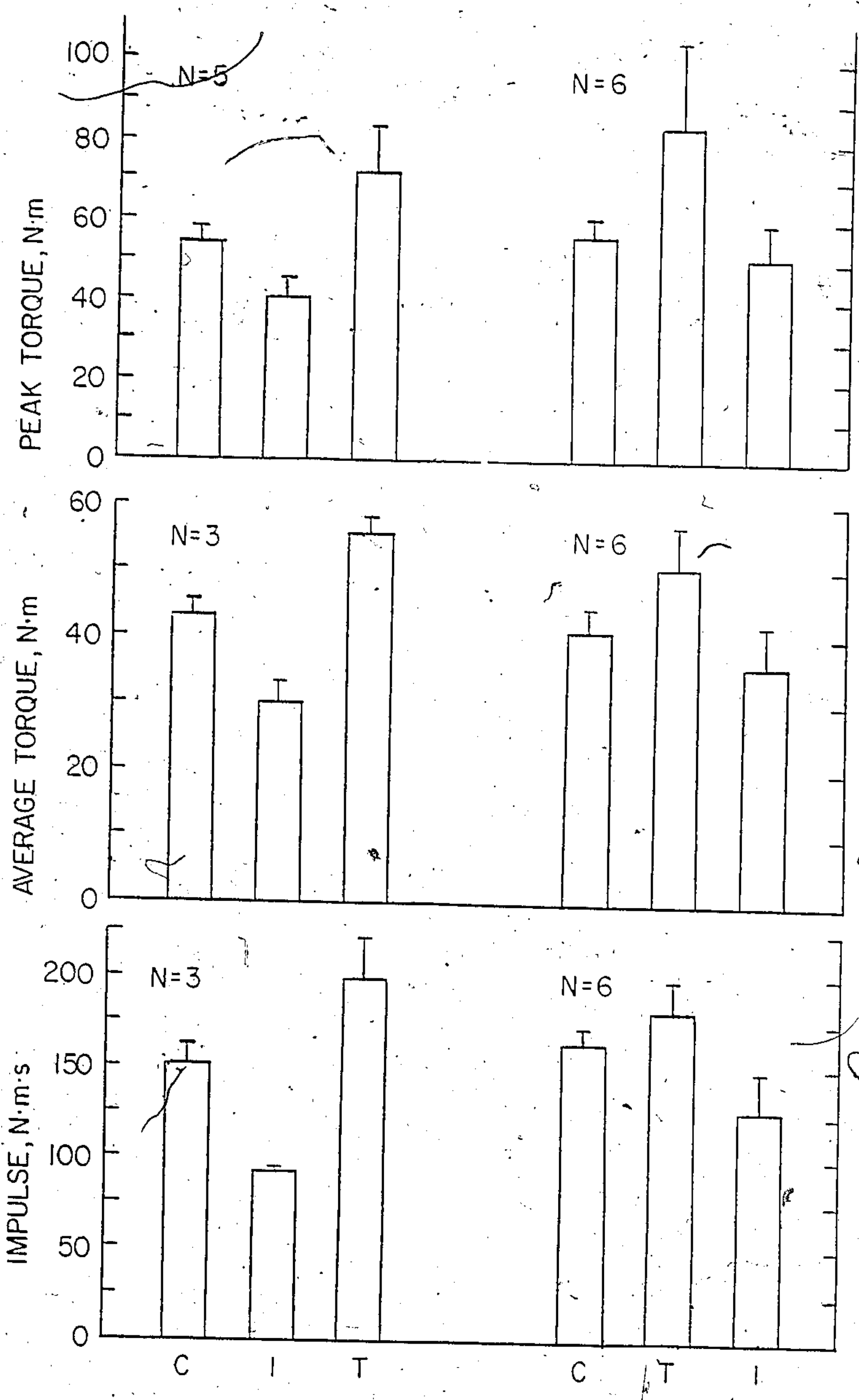

PEAK TORQUE, N·m
100
80
60
40
20
0
N=5
N=6
AVERAGE TORQUE, N·m
60
40
20
0
N=3
N=6
IMPULSE, N·m·s
200
150
100
50
0
N=3
N=6
C
I
T
C
T
I

Table 35. Effect of training and immobilization upon elbow extension strength when the results of the group which immobilized first and those of the group which trained first were combined.

Measure	Control	Post training	Post immobilization
Peak torque, N.m (N = 11)	55.4±3.2	74.8±12.3	46.0±5.2
Average torque, N.m (N = 9)	41.7±2.5	52.3±4.4	33.9±4.3
Impulse, N.m.s (N = 9)	159.6±7.0	187.9±12.9	116.0±15.4

Values are $\bar{x}$±SE

value by 42% ($p<0.05$) in peak torque, 25% ($p<0.005$) in average torque and by 18% ($p<0.02$) in impulse. The post training value exceeded the post immobilization value by 69% ($p<0.005$) in peak torque, 54% ($p<0.001$) in average torque and by 62% ($p<0.001$) in impulse. The post immobilization value was less than the control value by 16% ($p<0.05$) in peak torque, 19% ($p<0.02$) in average torque and by 27% ($p<0.005$) in impulse.

A total of seven subjects trained without prior immobilization. Peak torque increased by 48% (NS) from ($\bar{x}\pm SE$) 54.6±4.7 N.m to 80.8±18.4 N.m. Average torque increased by 21% ($p<0.05$) from 41.1±3.1 N.m to 49.8±5.6 N.m. Impulse increased by 10% (NS) from 163.5±8.0 N.m.s to 179.6±14.4 N.m.s.

A total of 13 subjects trained elbow extension. Six of these subjects immobilized prior to training. In relation to the control value, peak torque ($\bar{x}\pm SE$) increased by 39% ($p<0.05$) from 54.1±2.8 to 75.2±10.6 N.m. Average torque increased by 18% ($p<0.01$) from 41.1±2.2 to 48.5±3.4 N.m. Impulse increased by 11% (NS, $p<0.10$) from 160.3±7.4 to 178.5±9.7 N.m.s. Immobilization occurring prior to training did not significantly affect the response to training, when the training increase was expressed in relation to control values.

Six subjects who trained on the Cybex as well as with the weights were compared, in their training response as measured on the Cybex, with six subjects who trained with the weights only. In each group, half the subjects trained prior to immobilization, and half trained after immobilization. The Cybex-trained group in relation to control values made increases of 73% ($p<0.05$), 29% ($p<0.01$) and 25% ($p<0.02$) in peak torque, average torque and impulse respectively. The group which trained with weights only made non-significant increases of

9%, 5% and -1% in peak torque, average torque and impulse respectively. The training response of the Cybex group was significantly ($p<0.05$) greater than that of the group which trained with weights only.

In the group (N = 6) which trained on the Cybex, strength was tested on several occasions during the training period. The individual training response in four of these subjects is shown in Figures 18-21, and the group response is shown in Figure 22. When testing was done frequently (Figures 18 and 20), considerable day to day variation in performance was revealed; however, the average performance for the group increased progressively with time (Figure 22).

There was a positive correlation in the increase with training (N = 13) between peak torque and average torque ($r = 0.72$, $p<0.01$), between peak torque and impulse ($r = 0.59$, $p<0.05$) and between average torque and impulse ($r = 0.83$, $p<0.001$).

A total of seven subjects immobilized without a prior training period. Peak torque (N = 7) decreased by 26% ($p<0.001$) to 41.5±4.5 from 55.8±4.9 N.m ($\bar{x}$±SE). Average torque (N = 5) decreased by 26% ($p<0.005$) to 32.3±4.8 from 43.7±3.8 N.m. Impulse (N = 5) decreased by 36% ($p<0.001$) to 99.8±12.2 from 156.2±16.4 N.m.s.

A total of 13 subjects underwent immobilization. Six of the subjects trained prior to immobilization. In relation to the control value, peak torque (N = 13) decreased by 18% ($p<0.01$) to 46.0±4.6 from 55.8±3.~~4 N.m~~ ($\bar{x}$±SE). Average torque (N = 11) decreased by 19% ($p<0.005$) to 34.1±3.9 from 42.2±2.5 N.m. Impulse (N = 11) decreased by 28% ($p<0.001$) to 115.0±13.4 from 160.0±8.6 N.m.s. In the group which immobilized prior to training, peak torque decreased by 26% ($p<0.001$),

Figure 18. Record of progress in training of elbow extension strength in subject DN.

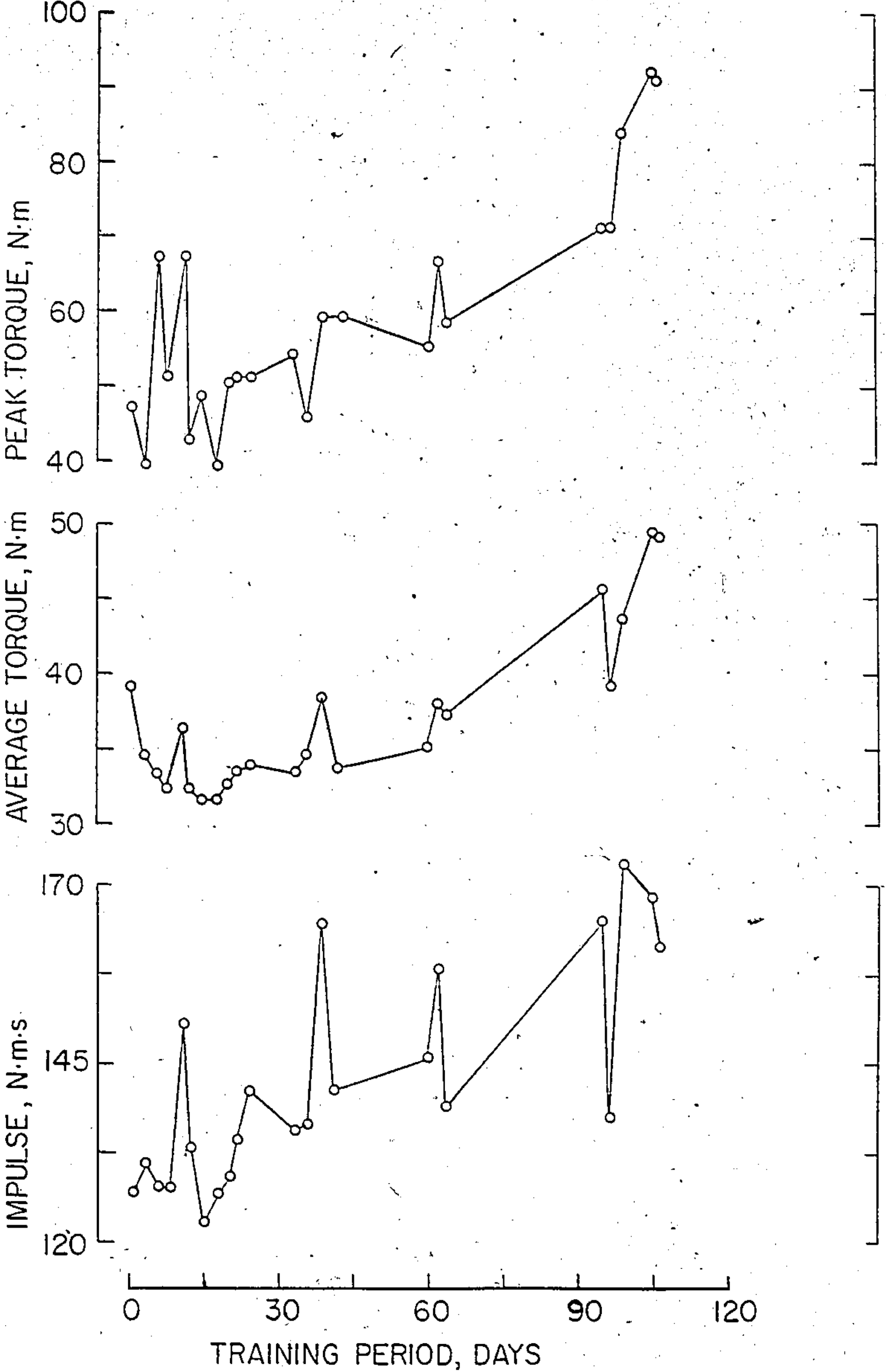

PEAK TORQUE, N·m
100
80
60
40
AVERAGE TORQUE, N·m
50
40
30
IMPULSE, N·m·s
170
145
120
0
30
60
90
120
TRAINING PERIOD, DAYS

Figure 19. Record of progress in training of elbow extension strength in subject BD.

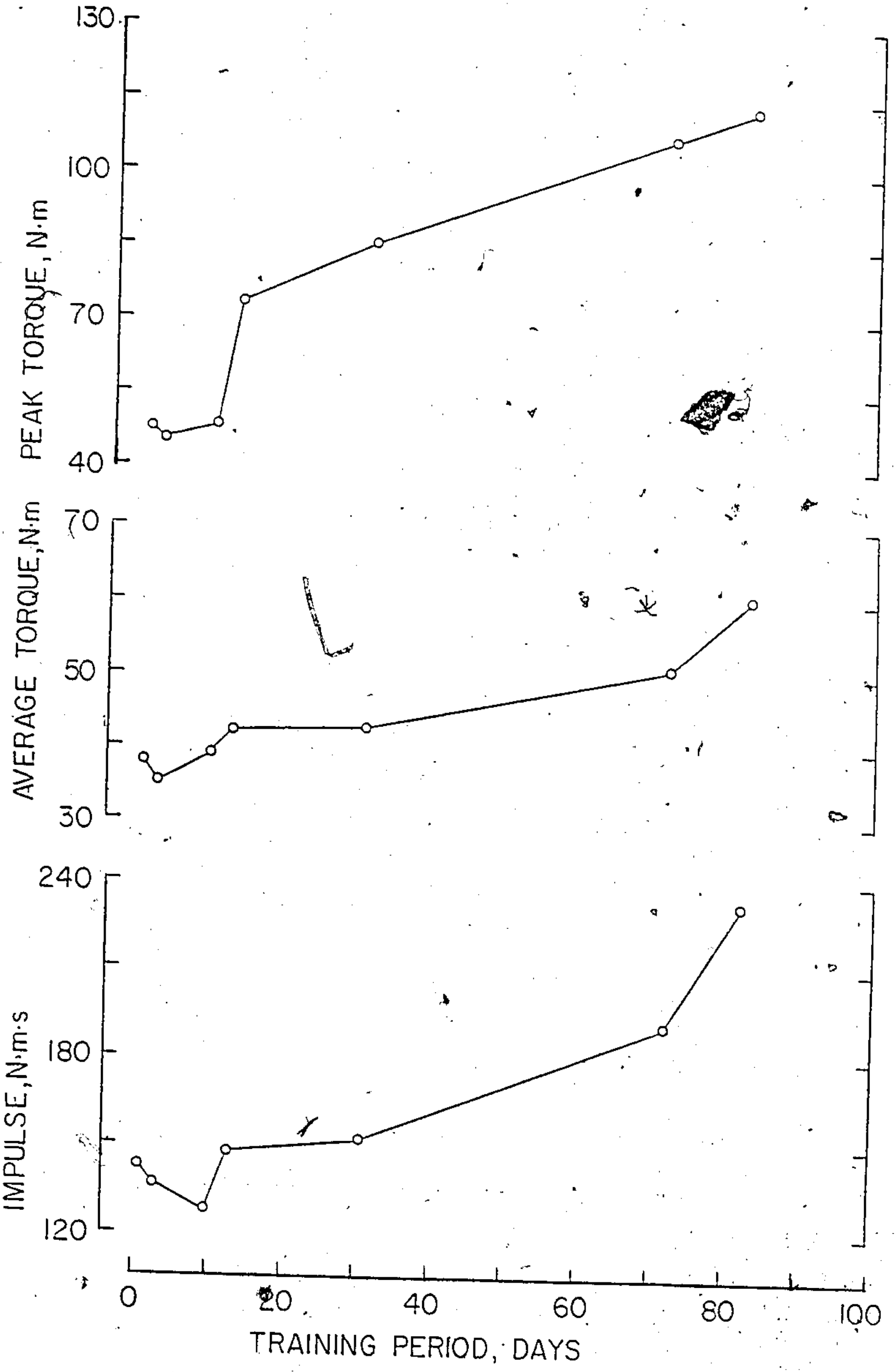

130
100
70
40
PEAK TORQUE, N·m
70
50
30
AVERAGE TORQUE, N·m
240
180
120
IMPULSE, N·m·s
0
20
40
60
80
100
TRAINING PERIOD, DAYS

Figure 20. Record of progress in training of elbow extension strength in subject WC.

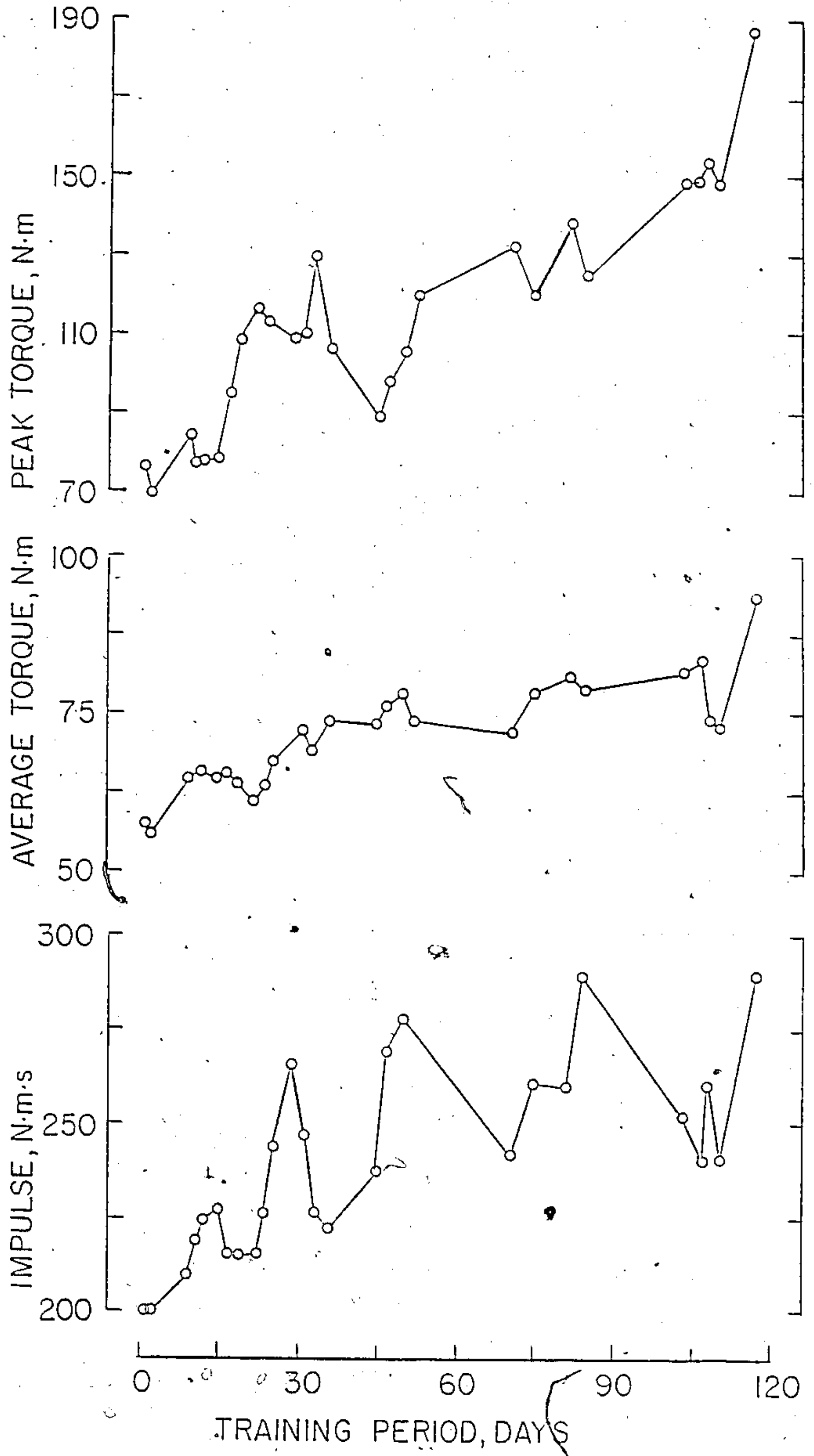

190
150
110
70
PEAK TORQUE, N·m
100
75
50
AVERAGE TORQUE, N·m
300
250
200
IMPULSE, N·m·s
0
30
60
90
120
TRAINING PERIOD, DAYS

Figure 21. Record of progress in training of elbow extension strength in subject SH.

21

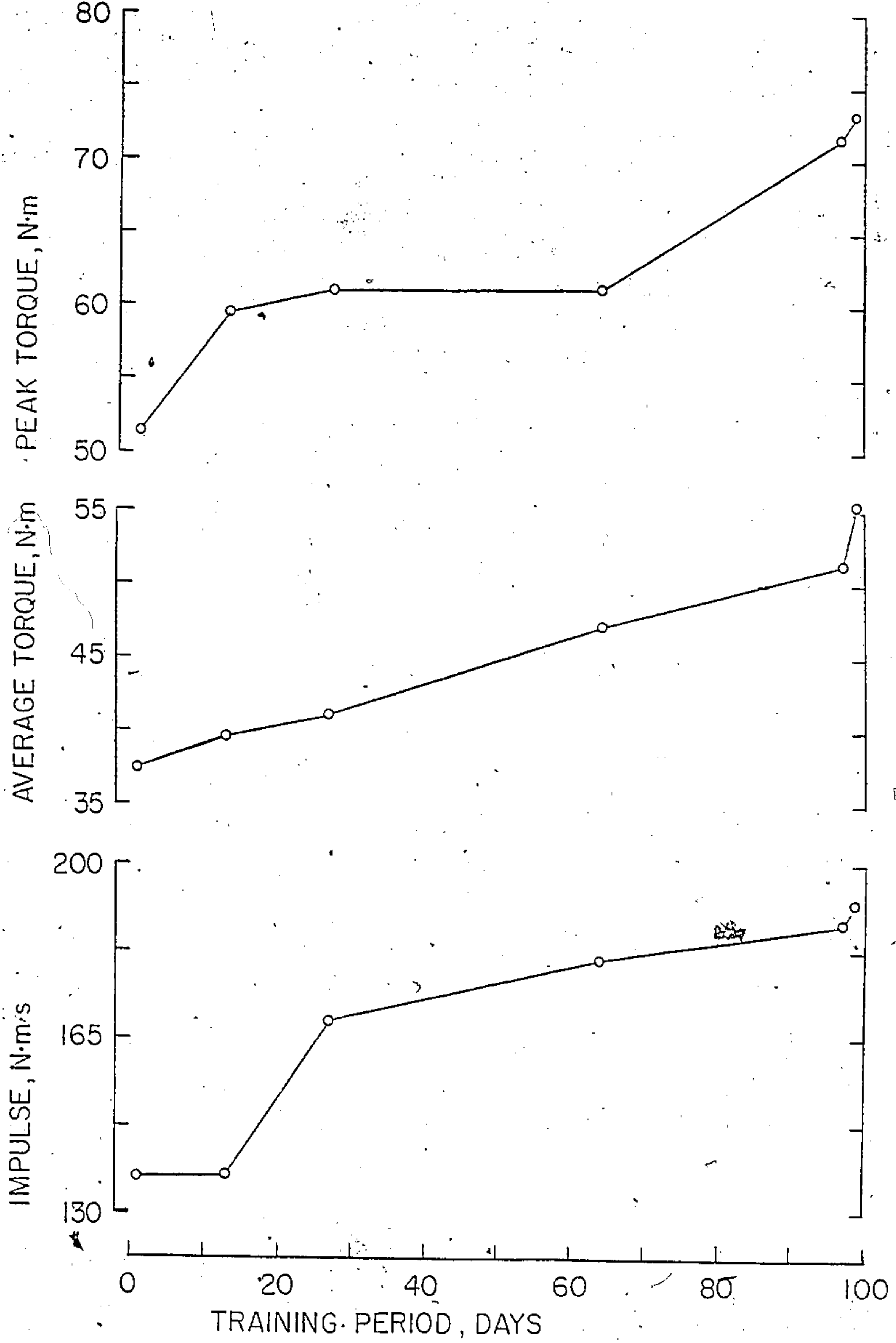
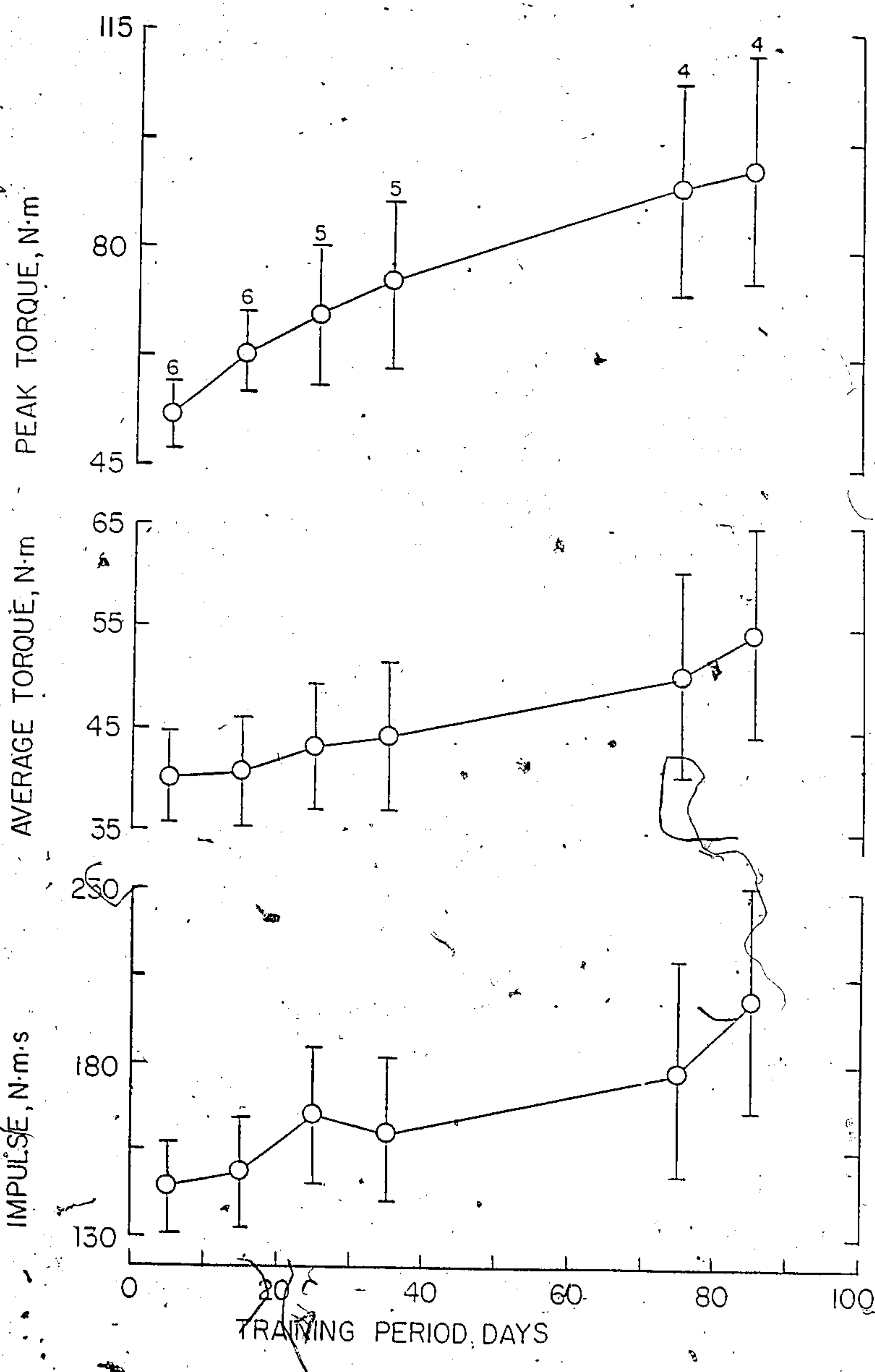

80
70
60
50
PEAK TORQUE, N·m
55
45
35
AVERAGE TORQUE, N·m
200
165
130
IMPULSE, N·m·s
0
20
40
60
80
100
TRAINING PERIOD, DAYS

Figure 22. Record of progress in training of elbow extension strength (N = 6). Values are $\bar{X} \pm$ SE.

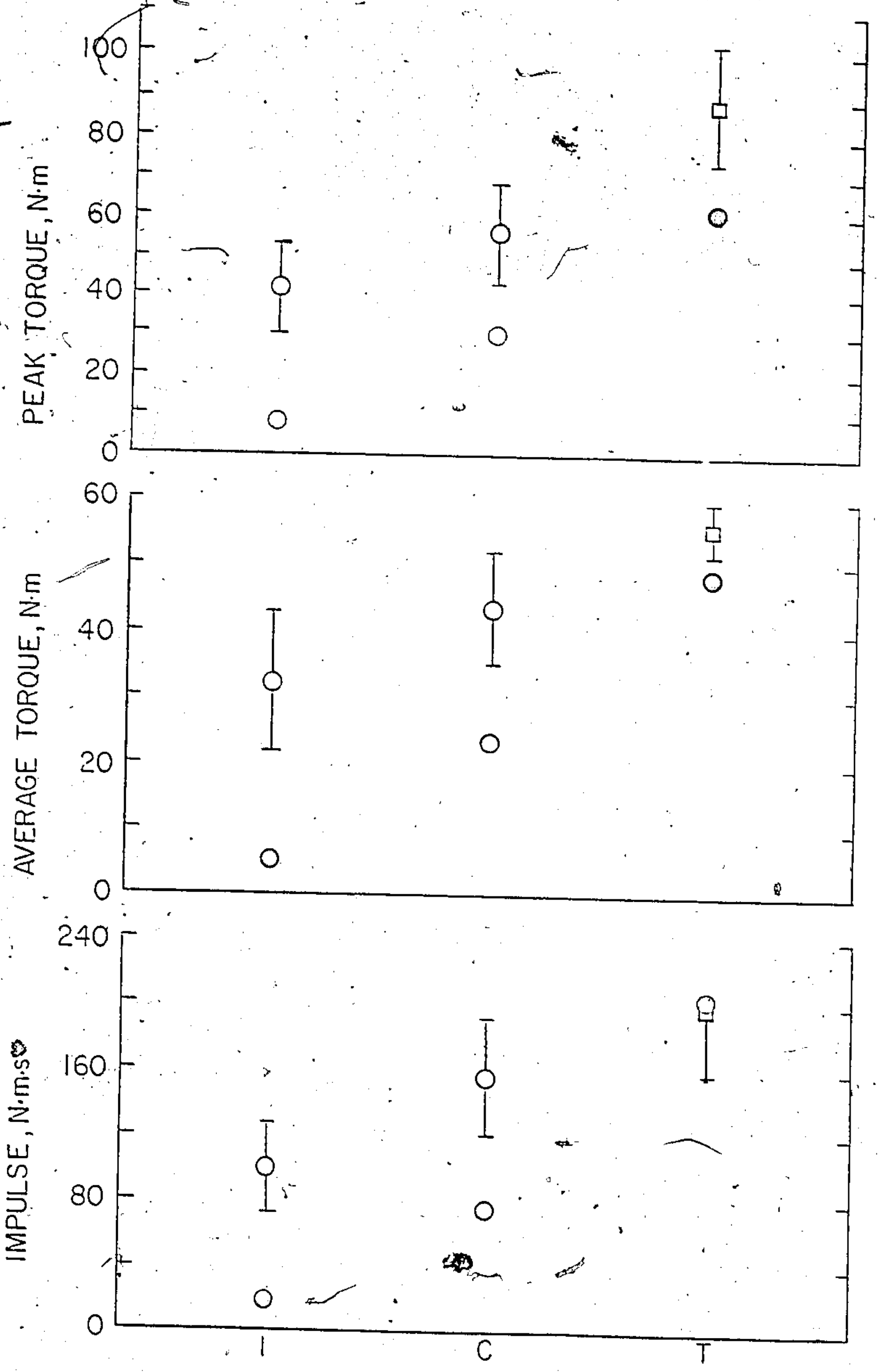

115
80
45
PEAK TORQUE, N·m
6
6
5
5
4
4
65
55
45
35
AVERAGE TORQUE, N·m
250
180
130
IMPULSE, N·m·s
0
20
40
60
80
100
TRAINING PERIOD, DAYS

average torque decreased by 26% ($p<0.005$) and impulse decreased by 36% ($p<0.001$) in relation to control values. In the group which trained prior to immobilization, peak torque, average torque and impulse decreased by 8%, 13% and 22% respectively in relation to the control values; these decreases were not significant. The decrease in elbow extension strength, in relation to the control value, which occurred in the group which immobilized without prior training was not significantly greater than the decrease that occurred in ~~the~~ group which trained prior to immobilization.

There was a positive correlation in the decrease with immobilization ($N = 11$) between peak torque and impulse ($r = 0.73$, $p<0.02$) and between average torque and impulse ($r = 0.78$, $p<0.001$). The correlation between the decrease in peak torque and average torque ($r = 0.51$) was not significant.

An additional subject, CC, was investigated after sustaining a fracture of the humerus (Figure 23). Tested shortly after removal of the cast, his values for peak torque, average torque and impulse were 2.82, 2.53 and 2.95 SD respectively below the post immobilization means of those subjects ($N = 7$) who immobilized without prior training. After three months of normal recovery, peak torque, average torque and impulse had increased by 267%, 325% and 300% respectively; however, his values for peak torque, average torque and impulse were still 2.02, 2.41 and 2.20 SD respectively below the control means of the same group of subjects. After five months of training on the Cybex and with weights, peak torque, average torque and impulse increased further by 105%, 112% and 169% respectively, from the three month recovery values, and his values were now 0.41, 0.60 and 1.31 SD

Figure 25. Elbow extension strength performance in subject CC (○) who had sustained a fracture of the humerus. Values are shown shortly after removal of cast (I = immobilization), after three months of normal recovery (C = control) and after five months of training (T). Also shown, for comparison, are values ($\bar{X} \pm SD$) in a group of subjects (○; N = 7 for peak torque; N = 5 for average torque and impulse) which had immobilized prior to training. Their post immobilization (I) and control (C) values prior to immobilization are shown. For another group of subjects (□ , N = 3) which trained after immobilization, the post training values are given (T).


PEAK TORQUE, N·m
0
20
40
60
80
100
AVERAGE TORQUE, N·m
0
20
40
60
IMPULSE, N·m·s
0
80
160
240
I
C
T

respectively above the control means in the same group of subjects.

The effect of training and immobilization upon voluntary isometric strength of thumb abduction is shown in Figure 24. In the group which trained prior to immobilization, peak torque increased by 47% (NS) after training, and after immobilization decreased by 47% ($p<0.025$) from the post training value and by 22% (NS) from the control value.

In the group which immobilized prior to training, peak torque decreased by 56% ($p<0.01$) after immobilization, and after training increased by 204% (NS, $p<0.10$) over the post immobilization value and by 35% (NS) over the control value.

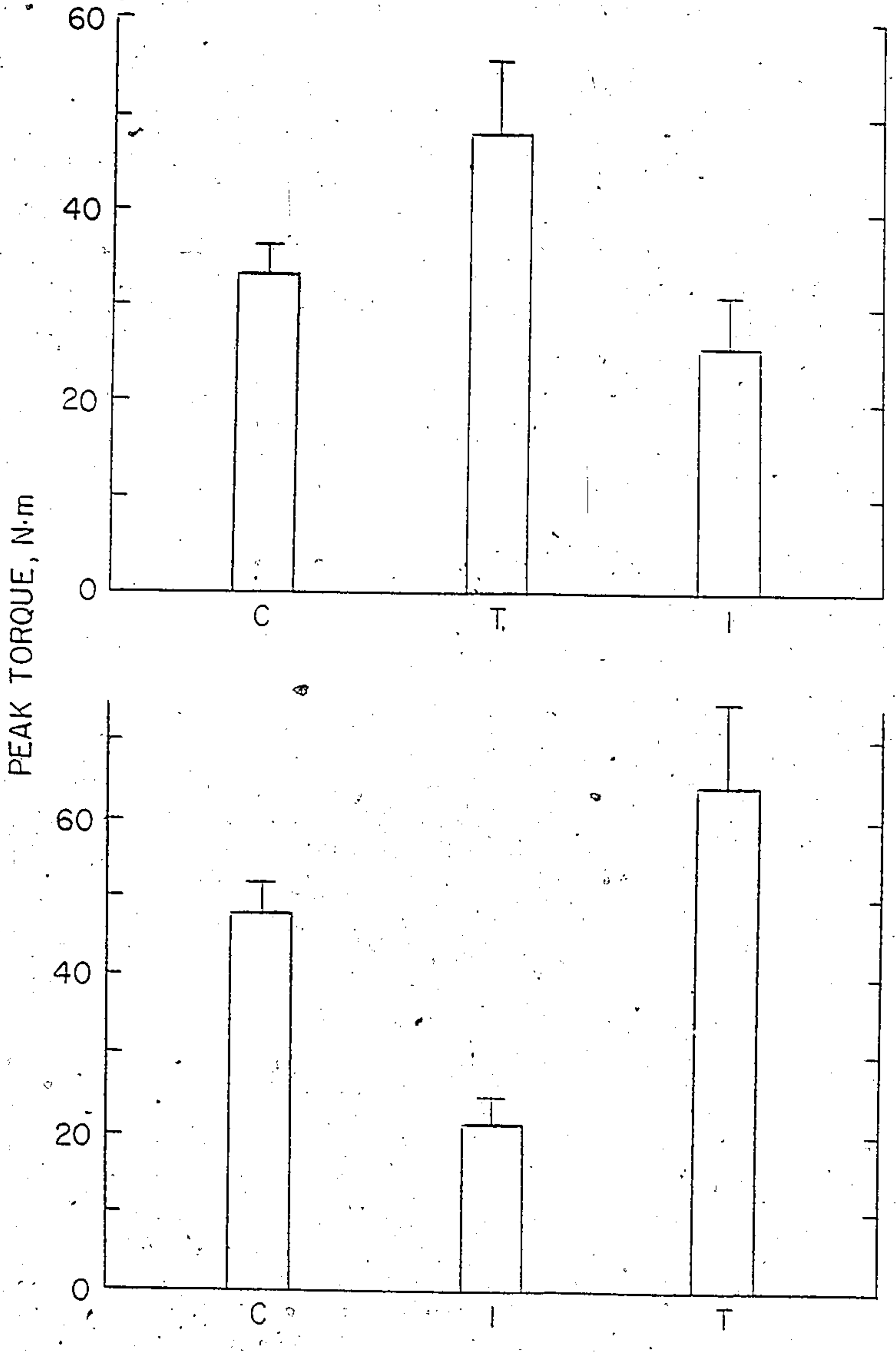
When the results of both groups were combined ($N = 6$), peak torque increased by 40% ($p<0.05$) to a post training value ($\bar{x}$±SE) of 56.5±6.9 N.m from the control value of 40.4±4.1 N.m. The post training value exceeded the post immobilization value of 23.5±3.2 N.m by 141% ($p<0.01$). The post immobilization value was less than the control value by 42% ($p<0.02$).

Whether the increase with training was expressed in relation to the control or post immobilization values, the training response of the group which trained prior to immobilization was not significantly different from the response of the group which immobilized prior to training.

Four subjects immobilized without prior training. Peak torque decreased by 57% ($p<0.001$) from a control value of 49.5±3.3 N.m to a post immobilization value of 21.4±2.6 N.m.

A total of seven subjects underwent immobilization. Three of the subjects trained prior to immobilization. Peak torque decreased by

Figure 24. Effect of training and immobilization upon voluntary isometric strength of thumb abduction. Top: a group (N = 3) which trained prior to immobilization. Bottom: a group (N = 3) which immobilized prior to training. Values are $\bar{X}$ and SE.


PEAK TORQUE, N·m
60
40
20
0
C
T
I
60
40
20
0
C
I
T

45% ($p<0.01$) from a control value of 42.4±4.0 N.m to a post immobilization value of 23.2±2.7 N.m.

In relation to the control value, the peak torque of the group (N = 4) which immobilized without prior training decreased by 57% ($p<0.001$) after immobilization, whereas the peak torque of the group which trained prior to immobilization decreased by 22% (NS) after immobilization. The decrease with immobilization was significantly less ($p<0.01$) for the group which trained prior to immobilization.

In six subjects, both elbow extension and thumb abduction strength were measured after training and immobilization. With respect to changes in strength caused by training and immobilization, the only significant correlation was between the increase in the peak torque of thumb abduction after training, in relation to the post immobilization value, and the corresponding increase in average torque of elbow extension ($r = 0.91$, $p<0.02$).

In three subjects, thumb abduction and elbow extension strength were measured after training and immobilization and after one and seven days of recovery from immobilization (Table 36). In both thumb abduction and elbow extension, the value for immediate post immobilization was similar to the value for one day of recovery from immobilization. After seven days of recovery, thumb abduction strength had returned to the initial control value, while elbow extension strength had surpassed the initial control value.

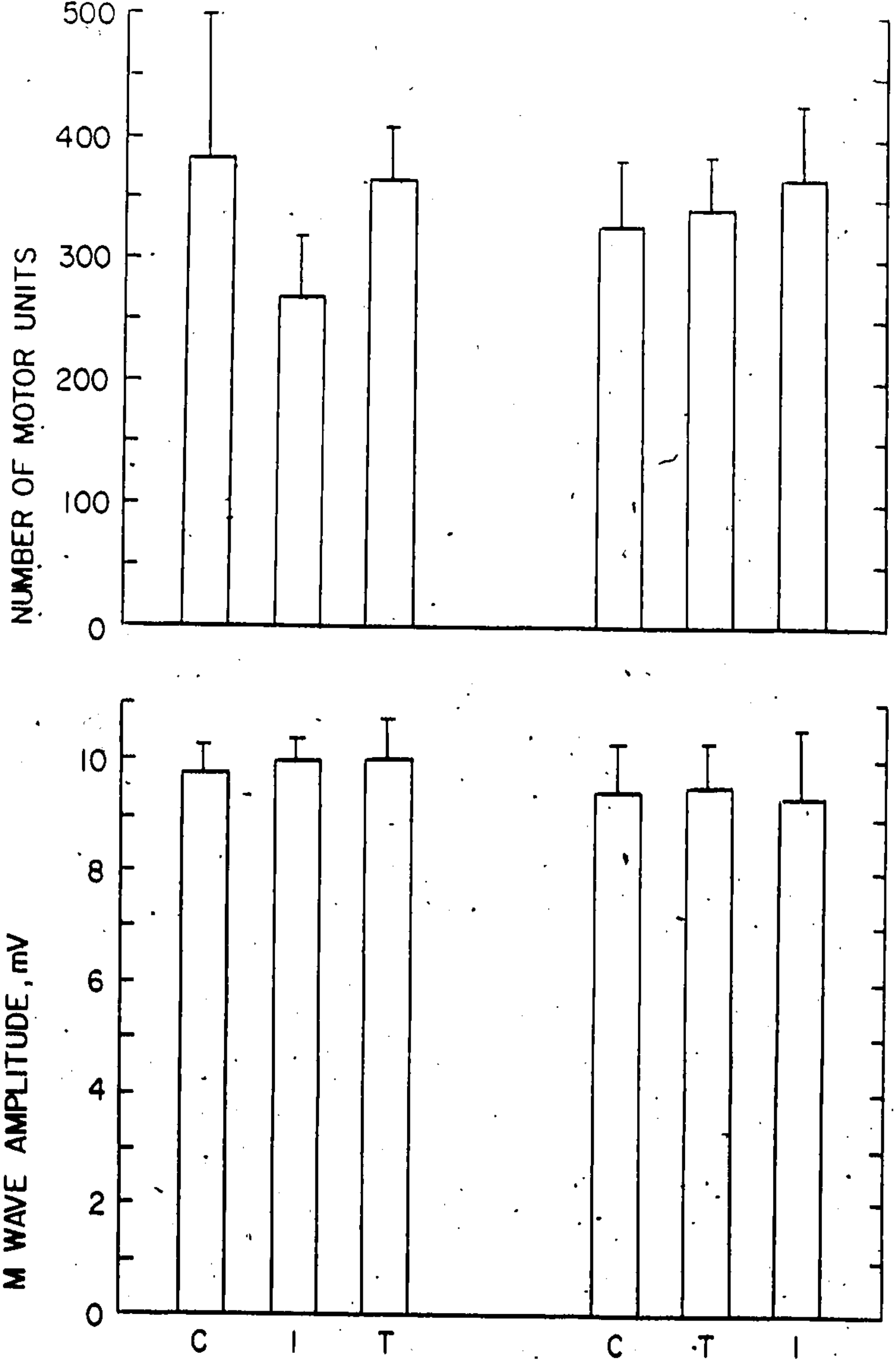
2. Motor Unit Counts. The results for subjects in whom thenar motor units and M wave amplitude were measured after both training and immobilization are shown in Figure 25. In the group which immobilized

Table 36. Effect of training, immobilization and recovery upon thumb abduction and elbow extension strength in three subjects.

Measure	Control	Training	Immobilization	Recovery	
				24h	7d
Thumb abduction Peak torque, N.m	32.5±2.7	48.8±8.1	25.8±5.4	25.8±6.8	32.5±8.1
Elbow extension Peak torque, N.m	58.3±9.5	109.8±40.7	63.7±13.6	63.7±12.2	67.8±20.3

Values are $\bar{x}$±SE

Figure 25. Effect of training (T) and immobilization (I), in relation to control values (C), upon thenar motor unit counts (top) and M wave amplitude (bottom). Left: a group (N = 5) which immobilized prior to training. Right: a group (N = 6) which trained prior to immobilization. Values are $\bar{X}$ and SE.


NUMBER OF MOTOR UNITS
500
400
300
200
100
0
M WAVE AMPLITUDE, mV
10
8
6
4
2
0
C
I
T
C
T
I

prior to training, the motor unit count decreased by 30% (NS) after immobilization, and after training, increased by 36% ($p<0.02$) over the post immobilization value and by 4% (NS) over the control value. In the group which trained prior to immobilization, the observed changes were small (≤ 13%) and not significant. In both groups, changes in M wave amplitude were small (≤ 4%) and not significant.

When the results of both groups were combined, the control, post immobilization and post training motor unit counts were ($\bar{x}$±SE) 352±59, 322±41 and 352±36 respectively; there were no significant differences among the three conditions. The control, post immobilization and post training values for M wave amplitude were 9.6±0.5, 9.6±0.7 and 9.8±0.5 mV respectively; there were no significant differences among the three conditions.

When the results of the two groups were compared, there was no significant difference between the two groups in the difference between control and post training values or in the difference between control and post immobilization values for motor units and M wave amplitude. However, in the group which immobilized prior to training, the post immobilization value for motor unit counts was 27% ($p<0.02$) less than the post training value, while in the group which trained prior to immobilization, the post immobilization value was 8% (NS) greater than the post training value. The two groups differed significantly ($p<0.05$) in the difference between post training and post immobilization values; there was no corresponding significant difference between the two groups in M wave amplitude.

A total of six subjects immobilized without prior training. The thenar motor unit count decreased by 28% (NS) from a control value of 350±101 to a post immobilization value of 253±44. The control and post immobilization values for M wave amplitude were 9.3±0.6 and 9.4±0.7 mV respectively (1%, NS).

A total of 20 subjects participated in training experiments involving 30 muscles (thenar, N = 14; hypothenar, N = 3; extensor digitorum brevis, N = 2); brachioradialis, N = 4; soleus, N = 7). There was no effect of training upon motor unit counts (2%, NS) or M wave amplitude (1%, NS).

3. Motor Nerve Conduction Velocity. Five subjects immobilized prior to training. The control, post immobilization and post training values for median motor nerve conduction velocity were ($\bar{x}$±SE) 61.0±1.6, 59.2±1.0 and 60.8±1.3 m/s respectively. The differences among conditions were small (≤3%); however, the post training value was significantly ($p<0.05$) greater than the post immobilization value.

Six subjects trained prior to immobilization. The control, post training and post immobilization values were 60.3±1.5, 59.8±1.2 and 60.8±1.2 m/s respectively. The differences among conditions were small (≤ 2%) and non-significant.

When the results of both groups were combined the control, post training and post immobilization values were 60.6±1.0, 60.3±0.9 and 59.6±0.8 m/s respectively. The differences among conditions were small (<1%) and non-significant.

When the results of the two groups were compared, there was no significant difference between the two groups in the difference between control and post training values or in the difference between control and post immobilization values. However, in the group which immobilized prior to training, the post training value exceeded the post immobilization value by 3% ($p<0.05$), while in the group which trained prior to immobilization, the post training value was less than the post immobilization value by 2% (NS). The two groups differed significantly ($p<0.05$) in the difference between post training and post immobilization values.

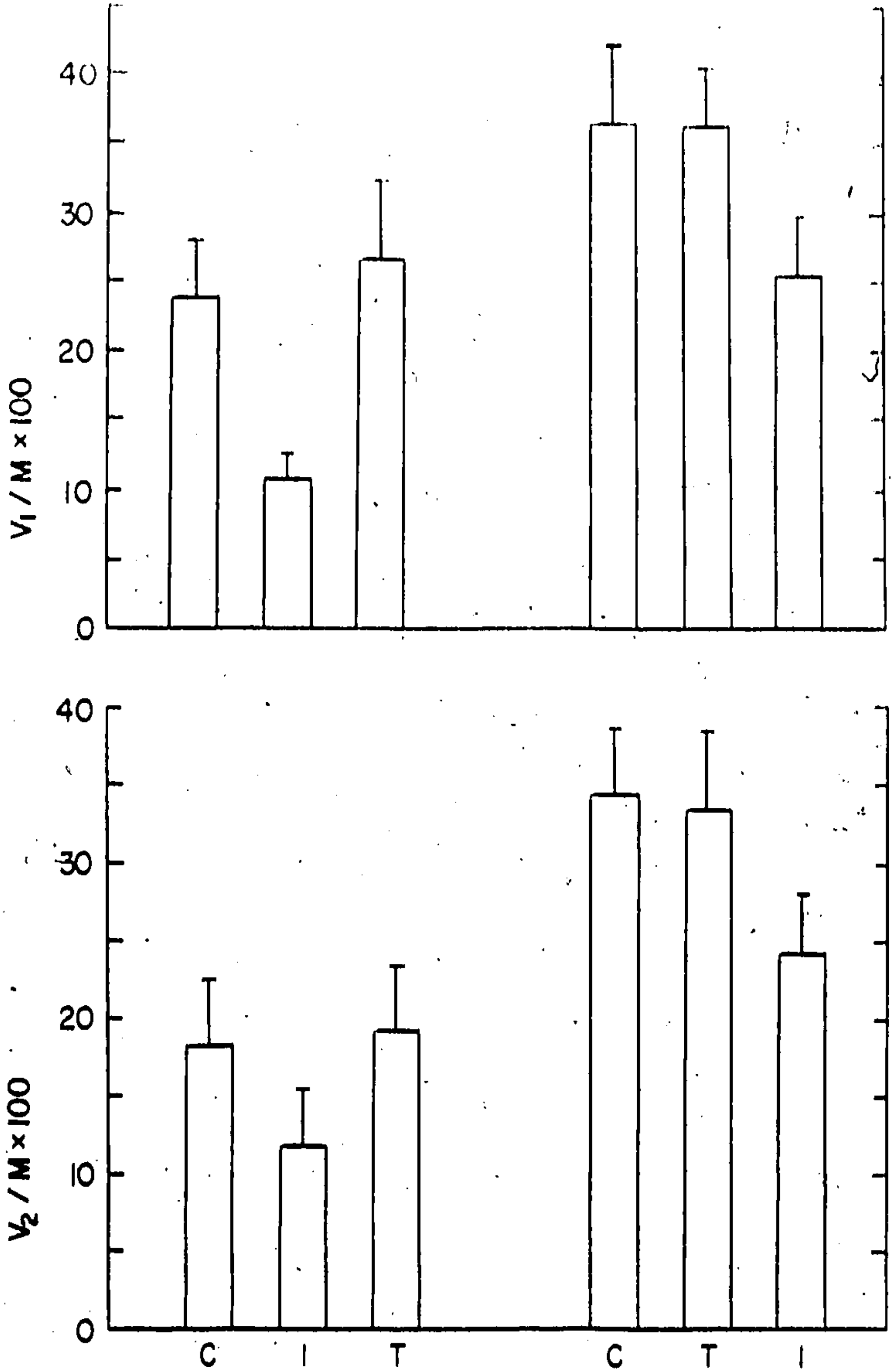
A total of six subjects immobilized without prior training. The control and post immobilization values for median motor nerve conduction velocity were 60.8±1.3 and 59.2±0.8 m/s respectively. The difference between conditions (2%) was not significant.

A total of 12 subjects underwent immobilization, six of whom trained prior to immobilization. The control and post immobilization values were 60.6±1.0 and 60.0±0.7 m/s respectively. The difference between conditions (1%) was not significant.

A total of 16 subjects participated in training experiments in which motor nerve conduction velocity was measured. A total of 20 muscles (nerves) were trained: thenar (median), N = 14; extensor digitorum brevis (deep peroneal), N = 3; hypothenar (ulnar), N = 3. There was no difference (< 1%, NS) between the control and post training values.

4. Reflex Potentiation. The results in the thenar muscles for those subjects who both trained and immobilized are presented in Figure 26. In the group (N = 6) which trained prior to immobilization, the V_1 value did not change (< 1%) after training, and after immobilization, decreased by 30% ($p<0.05$) from both the control and post training values. The V_2

Figure 26. Effect of immobilization (I) and training (T) upon potentiation of the V_1 (top) and V_2 (bottom) waves in thenar muscles (C = control values). Left: the results for the group (N = 5) which immobilized prior to training. Right: the results for the group (N = 6) which trained prior to immobilization. Values are $\bar{X}$ and SE.


40
30
20
10
0
$V_1 / M \times 100$
40
30
20
10
0
$V_2 / M \times 100$
C
I
T
C
T
I

value did not change significantly (3%) after training and after immobilization, decreased by 28% ($p<0.05$) from the post training value and by 30% ($p<0.005$) from the control value.

In the group (N = 5) which immobilized prior to training, the V_1 value decreased by 55% ($p<0.025$) from the control value, and after training increased by 148% ($p<0.02$) over the post immobilization value and by 13% (NS) over the control value. The V_2 value decreased by 35% ($p<0.005$) after immobilization, and after training increased by 61% ($p<0.05$) over the post immobilization value and by 6% (NS) over the control value.

When the results of both groups were combined, the control, post training and post immobilization V_1 values ($\bar{x}\pm SE$) were 30.8±4.0, 32.1±3.6 and 18.9±3.3 respectively. The post immobilization value was less by 37% and 41% ($p<0.001$) from the control value and post training value respectively. The post training value exceeded the control value by 4% (NS). The control, post training and post immobilization V_2 values were 27.1±3.9, 27.0±3.9 and 18.6±3.2 respectively. The post immobilization value was less by 31% from both the control ($p<0.001$) and post training ($p<0.005$) values.

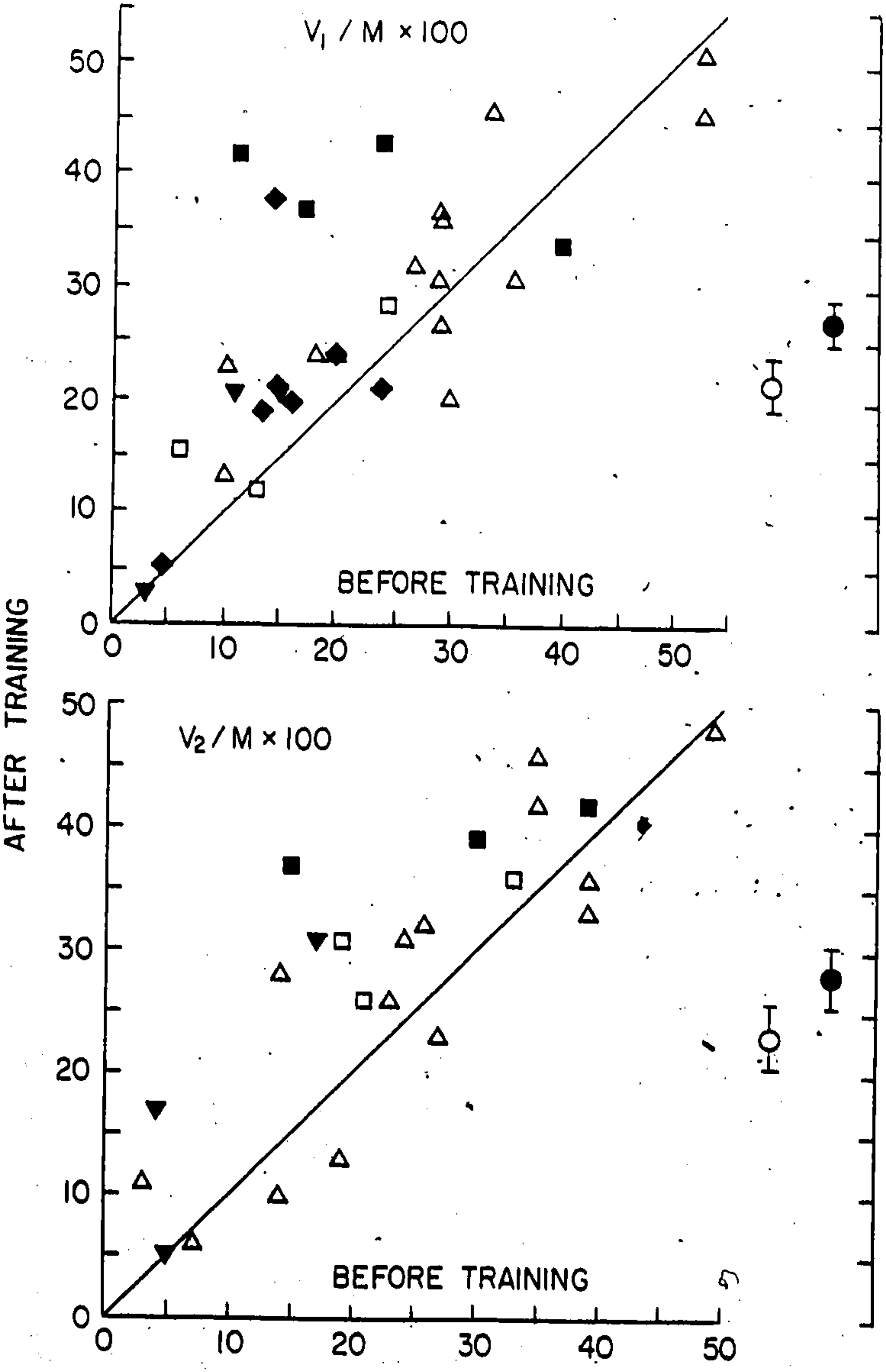
When the results of the two groups were compared, there was no significant difference between the two groups in the difference between control and post training values, between control and post immobilization values or between post training and post immobilization values for the V_1 and V_2 measures.

A total of six subjects immobilized the thenar muscles without prior training. The V_1 value decreased by 55% ($p<0.02$) from a control value ($\bar{x}$±SE) of 21.7±4.1 to a post immobilization value of 9.7±1.9. The V_2 value decreased by 33% ($p<0.01$) from a control value of 16.5±4.0 to a post immobilization of 11.1±3.0.

A total of 12 subjects underwent immobilization of the thenar muscles. Six of these subjects trained prior to immobilization. The V_1 value decreased by 39% ($p<0.001$) from a control value of 29.2±4.0 to a post immobilization value 17.1±3.2. The V_2 value decreased by 31% ($p<0.001$) from a control value of 25.5±3.0 to a post immobilization value of 17.6±3.1. There was no correlation in the decrease with immobilization, in relation to either the control or post training values, between the V_1 and V_2 values.

A total of 20 subjects, who trained 31 muscles (thenar, N = 14; hypothenar, N = 3; soleus, N = 7; extensor digitorum brevis, N = 3; brachioradialis, N = 4) participated in training experiments in which V_1 values were measured. The results are shown in Figure 27 (top). The overall result was a 25% ($p<0.005$) increase with training. A total of 19 subjects, who trained 23 muscles (thenar, N = 14; hypothenar, N = 3; extensor digitorum brevis, N = 3; brachioradialis, N = 3) participated in training experiments in which V_2 values were measured. The results are shown in Figure 27 (bottom). The overall result was a 21% ($p<0.005$) increase with training. There was a positive correlation ($r = 0.54$, $p<0.01$, N = 23) in the increase with training between V_1 and V_2 values.

Figure 27. Effect of training upon reflex potentiation. Individual values of V_1 (top) for 31 muscles trained in 20 subjects and V_2 (bottom) for 23 muscles trained in 19 subjects are shown along with the line of identity. Muscles trained included thenar (△), hypothenar (▼), soleus (◆), extensor digitorum brevis (□) and brachioradialis (■). To the right of the figure are shown the overall values ($\bar{X} \pm$ SE) before (○) and after (●) training.


V1 / M × 100
50
40
30
20
10
0
0
10
20
30
40
50
BEFORE TRAINING
AFTER TRAINING
V2 / M × 100
50
40
30
20
10
0
0
10
20
30
40
50
BEFORE TRAINING

In seven subjects, reflex potentiation in the thenar muscles was measured at various times during recovery after immobilization terminated. The results are shown in Table 37. V_1 potentiation appeared to recover at a faster rate than V_2 potentiation.

5. Muscle Twitch Properties. The results for those subjects who both trained and immobilized are presented in Figures 28 and 29. In the group (N=4) which immobilized prior to training, twitch tension increased by 2% (NS) after immobilization, and after training decreased by 33% (NS) from the post immobilization value and by 31% (NS, $p < 0.10$) from the control value. Contraction time increased by 9% (NS) after immobilization and after training decreased by 16% (NS) from the post immobilization and by 8% (NS) from the control value. Half relaxation time increased by 4% (NS) after immobilization, and after training decreased by 13% (NS) from the post immobilization value and by 9% (NS) from the control value. Rate of tension development decreased by 9% (NS) after immobilization, and after training decreased by 18% (NS) from the post immobilization value and by 25% (NS) from the control value.

In the group (N=6) which trained prior to immobilization, twitch tension decreased by 19% (NS, $p < 0.10$) after training, and after immobilization increased by 36% (NS) over the post training value and by 9% (NS) over the control value. Contraction time decreased by 8% ($p < 0.05$) after training, and after immobilization increased by 12% (NS) over the post training value and by 3% (NS) over the control value. Half relaxation time increased by 10% (NS) after training, and after immobilization increased by 11% (NS) over the post training value and by 21% (NS) over the control value. Rate of tension development

TABLE 37. Reflex potentiation in thenar muscles during recovery after termination of immobilization. V_1 and V_2 values are expressed as a percentage of control values.

	Post immobilization	Recovery		
		4-24h	4-7d	21d
Measure	(N = 7)	(N = 4)	(N = 4)	(N = 2)
V_1	63±10	79±30	84±11	91±0.01
V_2	57±8	56±17	76±7	80±6

Values are $\bar{x}$±SE

Figure 28. Effect of training (T) and immobilization (I) upon twitch tension (top), contraction time (middle) and half relaxation time in thenar muscles (C = control values). Left: a group (N = 4) which immobilized prior to training. Right: a group (N = 6) which trained prior to immobilization. Values are $\bar{X}$ and SE.

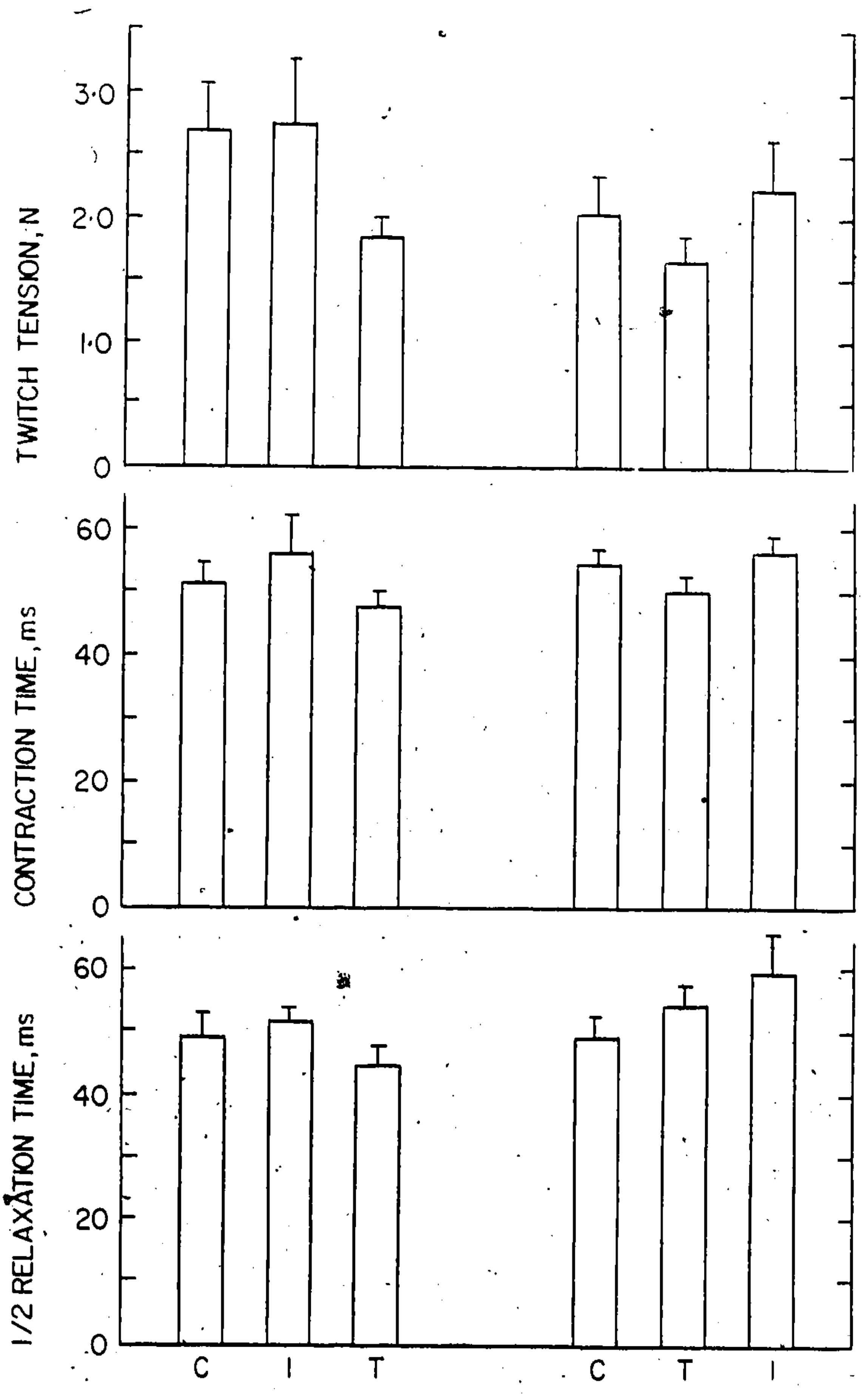
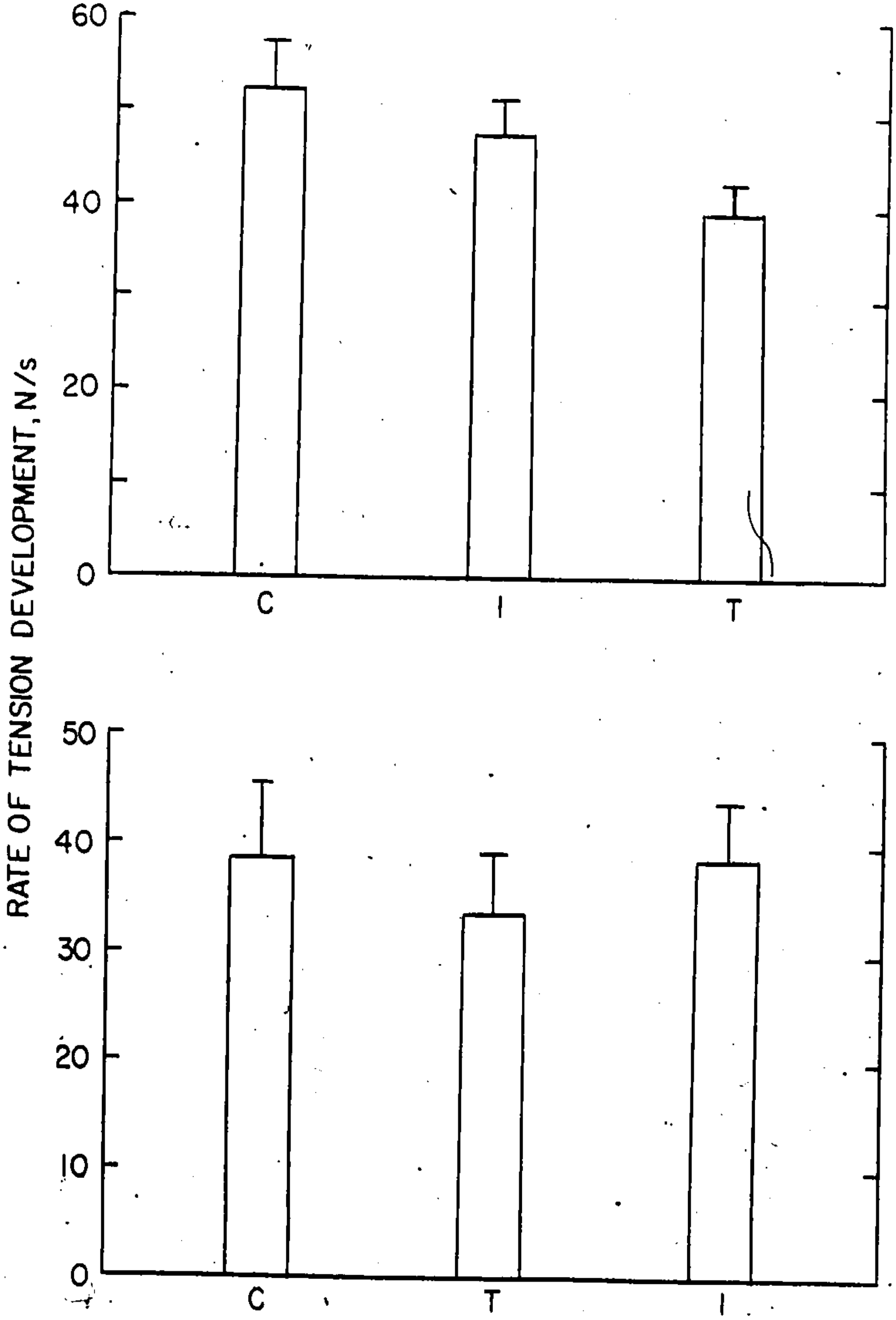

TWITCH TENSION, N
3·0
2·0
1·0
0
CONTRACTION TIME, ms
60
40
20
0
1/2 RELAXATION TIME, ms
60
40
20
0
C
I
T
C
T
I

Figure 29. Effect of training (T) and immobilization (I) upon rate of twitch tension development in thenar muscles (C = control values). Top: a group (N = 4) which immobilized prior to training. Bottom: a group (N = 6) which trained prior to immobilization. Values are $\bar{X}$ and SE.


RATE OF TENSION DEVELOPMENT, N/s
60
40
20
0
C
I
T
50
40
30
20
10
0
C
T
I

decreased by 13%(NS) after training, and after immobilization increased by 15% (NS) from the post training value.

Table 38 presents the results of both groups combined (N=10). The post training value for twitch tension was less than the control value by 25% ($p < 0.01$) and less than the post immobilization value by 29% ($p < 0.05$). The post immobilization value exceeded the control value by 6% (NS). The post training value for contraction time was 8% ($p < 0.05$) less than the control value and 13% ($p < 0.025$) less than the post immobilization value. The post immobilization value exceeded the control value by 6% (NS). The post training value for half relaxation time exceeded the control value by 2% (NS) and was 11% ($p < 0.025$) less than the post immobilization value. The post immobilization value exceeded the control value by 14% (NS). The post training value for rate of tension development was 19% ($p < 0.05$) less than the control value and 15% (NS) less than the post immobilization value. The post immobilization value was 4% (NS) less than the control value.

In the changes in twitch properties between the control and post training conditions, there was a correlation between the change in tension and the change in rate of tension development ($r = 0.93$, $p < 0.001$). There were no other significant correlations among the twitch properties. In the changes between the control and immobilization conditions, there was a correlation between the change in twitch tension and the change in half relaxation time ($r = 0.70$, $p < 0.05$). There were no other significant correlations.

TABLE 38. Effect of training and immobilization upon twitch properties of thenar muscles when the results of the group (N = 4) which immobilized first and those of the group (N = 6) which trained first were combined.

Measure	Control	Post training	Post immobilization
Twitch tension, N	2.29±0.25	1.72±0.14	2.43±0.31
Contraction time, ms	53.1±1.8	49.0±1.8	56.0±2.7
Half relaxation time, ms	49.3±2.4	50.3±2.8	56.4±3.7
Rate of tension development, N/s	44.3±5.2	36.1±3.6	42.4±3.8

Values $\bar{X}$±SE

among the twitch properties. In the changes between the post training and post immobilization conditions, there was a correlation between the change in twitch tension and the change in contraction time ($r = 0.72$, $p < 0.02$), and a correlation between the change in tension and the change in rate of tension development ($r = 0.89$, $p < 0.001$). There were no other significant correlations among the twitch properties.

When the results of the two groups were compared, there was no significant difference between the two groups in the difference between control and post training values, between control and post immobilization values or between post training and post immobilization values of the twitch properties.

A total of five subjects immobilized without prior training. The post immobilization value for twitch tension of 2.73 ± 0.40 N exceeded the control value of 2.65 ± 0.29 by 3% (NS). The post immobilization value for contraction time of 55.0 ± 4.9 ms exceeded the control value of 53.7 ± 1.7 ms by 4% (NS). The post immobilization value for half relaxation time of 56.4 ± 5.4 ms exceeded the control value of 49.2 ± 2.9 ms by 15% (NS). The post immobilization value for rate of tension development of 48.78 ± 2.93 N/s was less than the control value of 50.41 ± 5.74 N/s by 3% (NS).

A total of 11 subjects underwent immobilization of the thenar muscles. Six of the subjects trained prior to immobilization. After immobilization, twitch tension increased by 6% (NS) from a control value of 2.31 ± 0.22 N to 2.45 ± 0.28 N. Contraction time increased by 4% (NS) from 53.7 ± 1.7 ms to 55.6 ± 2.5 ms. Half relaxation time increased by 18% ($p < 0.05$) from 49.3 ± 2.2 ms to 53.8 ± 3.9 ms. Rate of tension development decreased by 2% (NS) from 44.03 ± 4.69 N/s to 43.31 ± 3.50 N/s. There was a correlation between the increase in twitch tension and the increase in half relaxation time ($r = 0.62$, $p < 0.05$). There were no other significant correlations among the twitch properties.

A total of 13 subjects trained the thenar muscles. Four of the subjects immobilized prior to training. After training, twitch tension decreased by 23% ($p < 0.01$) from a control value of 2.23 ± 0.24 N to 1.72 ± 0.12 N. Contraction time decreased by 7% ($p < 0.02$) from a control value of 53.1 ± 1.4 ms to 49.5 ± 1.4 ms. Half relaxation time did not change after training. Rate of tension development decreased by 17% ($p < 0.05$) from a control value of 42.74 ± 4.82 N/s to 35.36 ± 2.92 N/s. There was a correlation between the decrease in twitch tension and the decrease in rate of tension development after training ($r = 0.95$, $p < 0.001$). There were no other significant correlations among the twitch properties.

Three subjects trained the hypothenar muscles and two subjects trained extensor hallucis brevis. The results in these muscles were added to those of the thenar muscles and are presented in Figures 30 and 31. The overall (N=18) mean twitch tension decreased by 21% ($p < 0.005$) after training. Contraction time decreased by 3% (NS) and half relaxation time did not change. Rate of tension development decreased by 18% ($p < 0.01$). When the results for the three muscles were combined, there was a correlation between the decrease in twitch

Figure 30. Effect of training upon muscle twitch properties. Top: individual values of twitch tension in thenar (△), hypothenar (□) and extensor hallucis brevis (◇) muscles are shown along with the line of identity. To the right of the figure are the overall mean (-SE) values before (○) and after (●) training. Bottom: individual values of contraction time (unfilled symbols) and half relaxation time (filled symbols) in thenar (△ , ▲), hypothenar (□ , ■) and extensor hallucis brevis (◇ , ◆) muscles along with the line of identity. To the right of the figure are shown the overall values ($\bar{X}$ ± SE) before (○ , contraction time; ▽ , half relaxation time) and after (filled symbols) training.

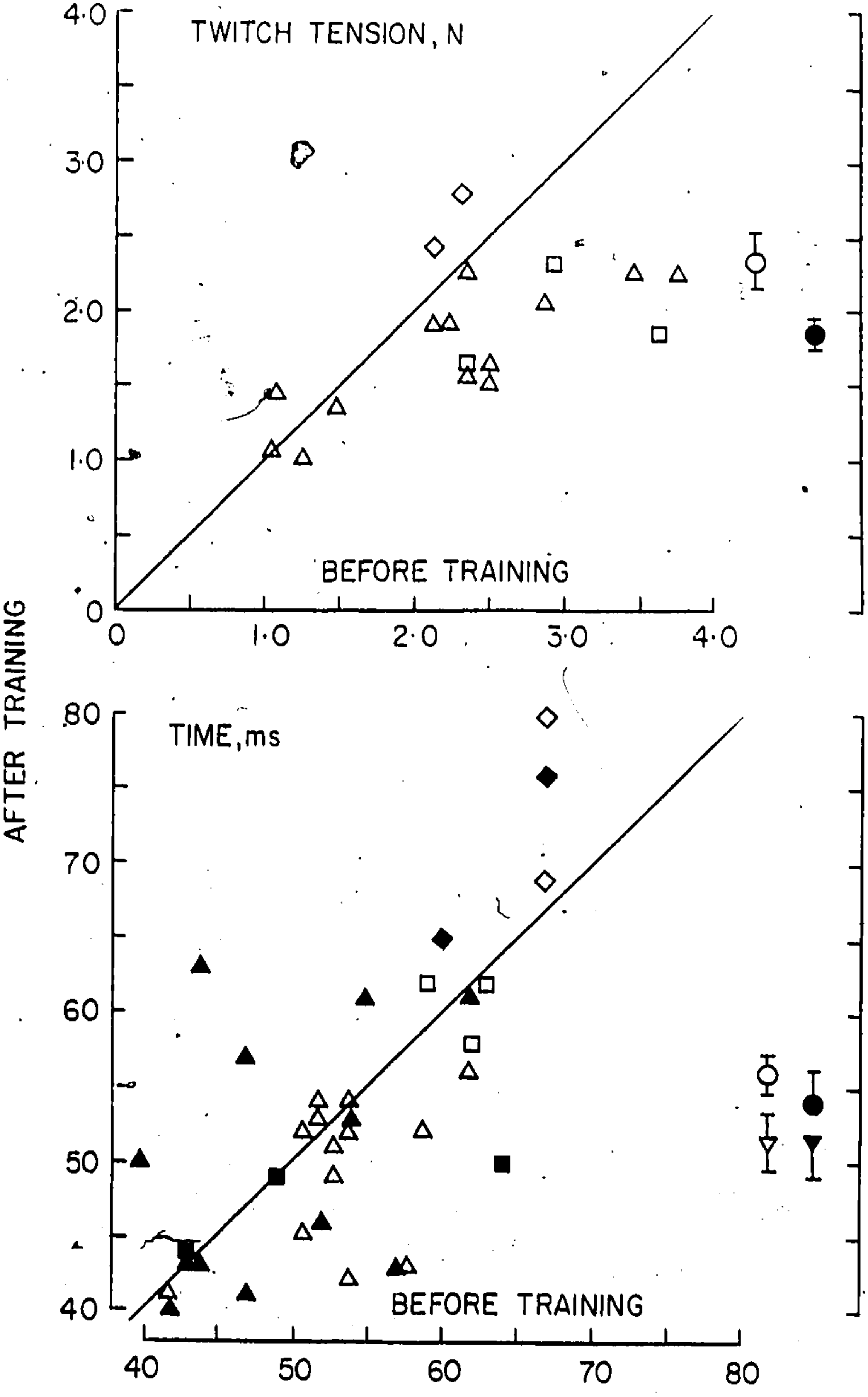
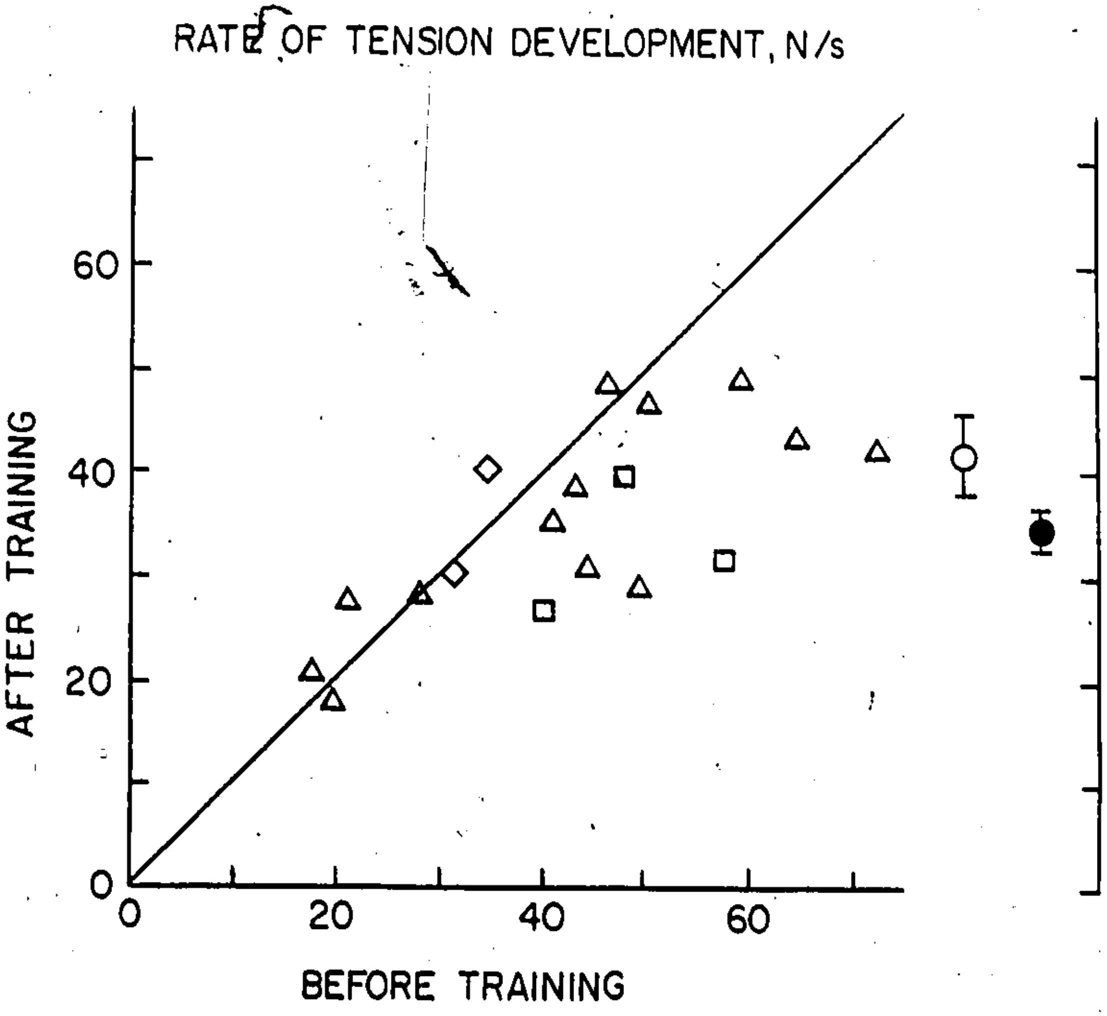

TWITCH TENSION, N
BEFORE TRAINING
AFTER TRAINING
0
1·0
2·0
3·0
4·0
TIME, ms
BEFORE TRAINING
40
50
60
70
80

Figure 31. Effect of training upon rate of twitch tension development. Individual values for thenar (△), hypothenar (□) and extensor hallucis brevis (◇) muscles are shown along with the line of identity. To the right of the figure are shown the overall values ($\bar{X} \pm$ SE) before (○) and after (●) training.


RATE OF TENSION DEVELOPMENT, N/s
AFTER TRAINING
BEFORE TRAINING
0
20
40
60
0
20
40
60

tension and the decrease in rate of tension development ($r = 0.94$, $p < 0.001$). There were no other significant correlations among the twitch properties.

Eight subjects trained triceps surae. After training twitch tension decreased by 2% (NS) from a control value of 96.4 ± 9.6 to 94.7 ± 9.4 N. Contraction time increased by 4% (NS) from 109.0 ± 3.8 ms to 113.5 ± 3.7 ms. Half relaxation time increased by 7% ($p < 0.025$) from 93.8 ± 4.1 ms to 100.9 ± 5.0 ms. Rate of tension development decreased by 9% ($p < 0.05$) from a control value of 889.3 ± 89.0 N/s to 831.1 ± 70.7 N/s. There was a negative correlation between the increase in contraction time and half relaxation time ($r = -0.87$; $p < 0.01$). There were no other significant correlations among the twitch properties.

6. Response of the Immobilized Thenar Muscles to Activity of Other Muscle Groups. Three of the subjects who underwent immobilization had small openings made in their casts so that electromyographic recordings could be made of the immobilized thenar muscles during activity of non-immobilized muscle groups. Observations were made in two of the subjects after five weeks of immobilization, and in the third subject after one week of immobilization. The results in two of the subjects are presented in Figures 32 and 33. The results were similar in all three subjects. Contraction of the finger flexors and elbow flexors of the non-immobilized limb was associated with an increase in motor unit activity in the immobilized thenar muscles. There was an apparent correlation between the force and duration of the contractions of the non-immobilized muscle groups and the degree of motor unit activity evoked in the immobilized thenar muscles. The greatest response of the immobilized thenar muscles occurred when the fingers of the immobilized limb were used to tie shoe laces.

Figure 32. Electromyographic recordings from the immobilized thenar muscles during contractions of other muscles. Recordings made on the left side in subject MA after one week of immobilization. A: all muscle groups at rest. B: 5s isometric contraction of the right finger flexors at a force equal to 50% MVC (maximal voluntary contraction). C: 60s isometric contraction of the right finger flexors at 50% MVC. D: 15s isometric contraction of the right finger flexors at 100% MVC. E: 5s isometric contraction of the right elbow flexors at 100% MVC. F: putting on a coat using the right arm only. G: tying shoe laces using the fingers of the left (immobilized) limb.

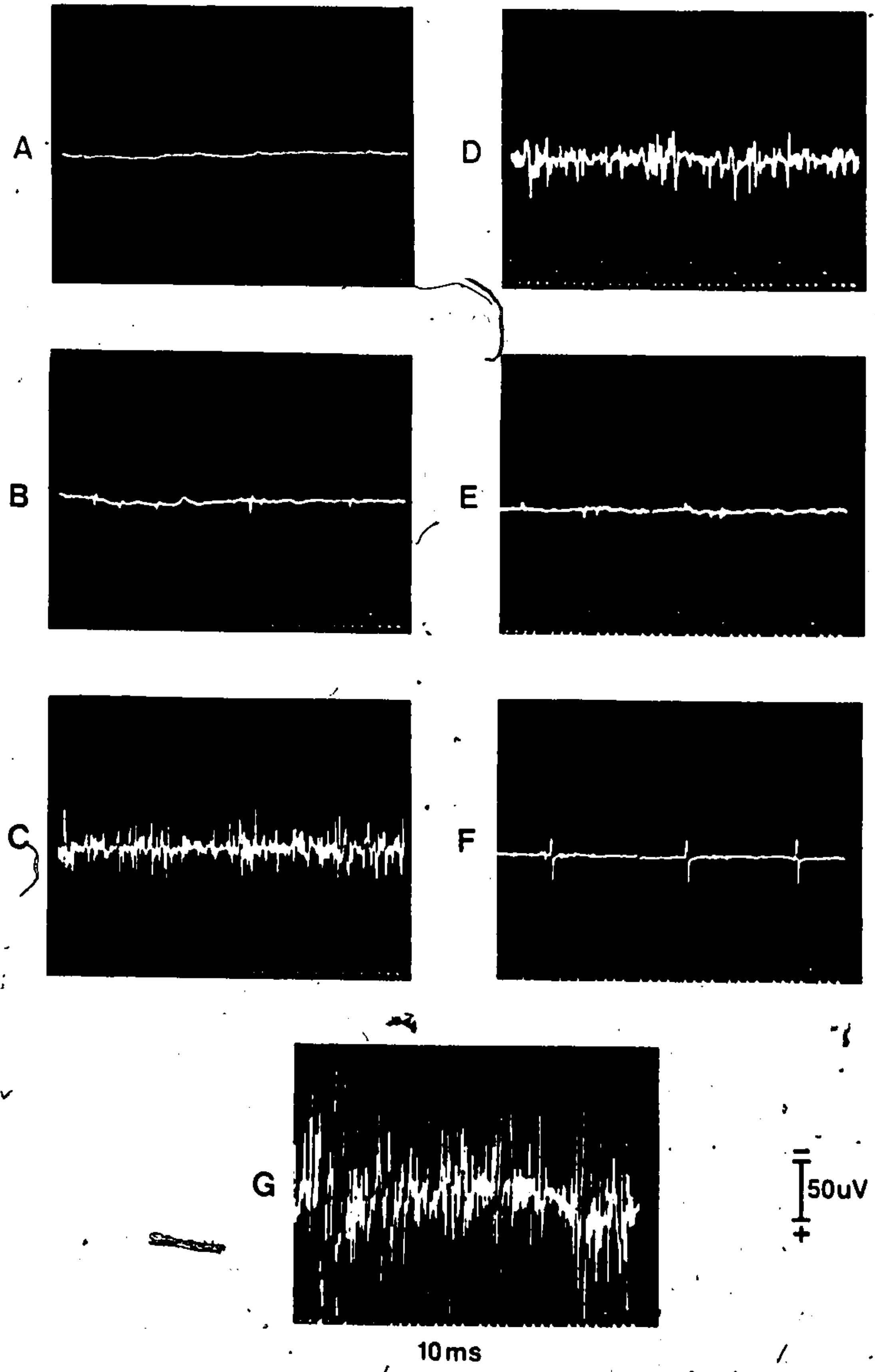
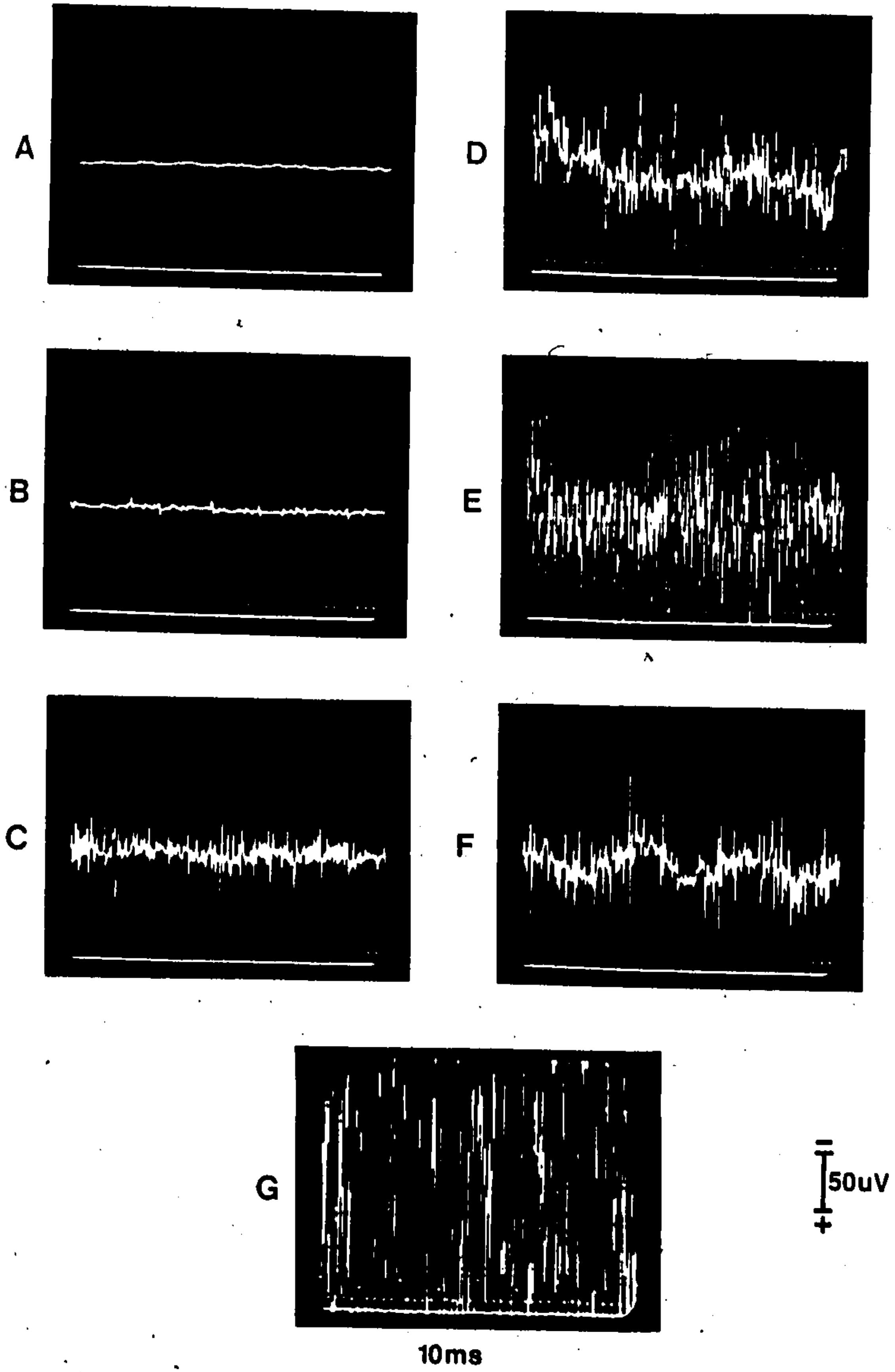

A
D
B
E
C
F
G
50uV
10ms

Figure 33. Electromyographic recordings from the immobilized thenar muscles during contractions of other muscles. Recordings made on the left side in subject SG after five weeks of immobilization. A: all muscle groups at rest. B: 5s isometric contraction of the right finger flexors at a force equal to 50% MVC (maximal voluntary contraction). C: 60s isometric contraction of the right finger flexors at 50% MVC. D: 5s isometric contraction of the finger flexors at 100% MVC. E: 15s isometric contraction of the right finger flexors at 100% MVC. F: 5s isometric contraction of the right elbow flexors at 100% MVC. G: tying shoe laces using the fingers of the left (immobilized) limb.


A
D
B
E
C
F
G
50uV
10ms

D. Voluntary Strength and Electrophysiological Measurements in Weight Trainers

The results of measurements in weight trainers are presented with corresponding results in control subjects.

1. Anthropometric Measurements. The results of anthropometric measurements in weight trainers and control subjects are presented in Table 39. The control subjects were 2% taller on the average than the weight trainers; however, the weight trainers were 21% heavier than the control subjects. When the values for the right and left sides were combined, calf, thigh and arm girth were greater in the weight trainers than in the controls by 5%, 12% and 25% respectively.

2. Voluntary Strength. The results of the voluntary strength measurements in weight trainers and control subjects are presented in Tables 40 and 41. In Figure 34, the mean values for voluntary strength and anthropometric measurements in weight trainers have been expressed as a proportion of the corresponding values in control subjects. The weight trainers' values exceeded the control values to the greatest extent in arm girth and elbow extension strength, and to the least extent in calf girth and ankle plantar flexion strength. The correlations between strength and height, mass and limb girth are presented in Tables 42-44. The correlations between strength and the anthropometric measurements were greatest for elbow extension and smallest for ankle plantar flexion. There was a notable lack of correlation in all three movements between strength and height.

In all three movements, there was a positive correlation between body mass and strength. When the strength values were expressed per kg body mass rather than absolutely, the difference between the

TABLE 39. Anthropometric measurements in weight trainers and control subjects.

Measure	Controls	Weight trainers	Diff.	p
Height, cm	177.5±1.1 (25)	174.5±1.6 (16)	3.0	NS
Mass, kg	71.7±1.5 (25)	86.4±2.5 (16)	14.7	<0.001
Calf girth, cm				
right	37.3±0.4 (19)	39.2±0.6 (13)	2.0	<0.02
left	37.2±0.4 (19)	38.6±0.5 (12)	1.4	<0.05
Thigh girth, cm				
right	56.0±0.6 (19)	62.5±1.4 (12)	6.5	<0.001
left	55.6±0.6 (19)	62.3±1.4 (12)	6.7	<0.001
Arm girth, cm				
right	30.2±0.4 (19)	38.5±1.0 (15)	8.3	<0.001
left	30.2±0.3 (19)	37.0±0.8 (12)	6.8	<0.001

Values are $\bar{X}$ ± SE/(N)

TABLE 40. Voluntary strength measurements in weight trainers and control subjects. Values are expressed absolutely.

Measure	Left Controls	Left Weight trainers	Left Diff.	Right Controls	Right Weight trainers	Right Diff.
Ankle plantar flexion						
Peak torque, N.M.						
6 deg/s	240.4±10.6 (24)	280.0±26.7 (11)	39.6 (NS)	245.4±10.0 (25)	293.4±19.9 (12)	48.0 (< 0.05)
36 deg/s	126.5±7.6 (24)	151.3±18.3 (11)	24.8 (NS)	132.7±7.4 (25)	158.3±12.5 (12)	25.6 (NS)
Average torque, N.m.						
6 deg/s	144.3±8.1 (24)	161.6±18.1 (11)	17.3 (NS)	142.4±7.3 (25)	165.0±12.6 (12)	22.6 (NS)
36 deg/s	71.5±4.1 (24)	86.0±9.7 (11)	14.5 (NS)	73.7±4.3 (25)	88.9±6.8 (12)	15.2 (NS)
Impulse, N.m.s.						
6 deg/s	236.5±17.2 (24)	323.8±43.8 (11)	87.3 (NS)	251.1±15.2 (25)	309.0±32.3 (12)	57.9 (NS)

TABLE 40. Continued.

36 deg/s	32.2±3.7 (24)	40.7±7.0 (11)	8.5 (NS)	35.1±2.8 (25)	43.9±4.7 (12)	8.8 (NS)
Knee extension						
Peak torque, N.m.						
30 deg/s	185.8±5.4 (24)	232.6±10.7 (12)	46.8 (< 0.001)	202.5±7.2 (25)	243.4±13.1 (12)	40.9 (< 0.02)
180 deg/s	144.1±5.2 (24)	172.7±9.3 (12)	28.6 (< 0.02)	156.2±5.0 (25)	192.5±11.4 (12)	36.3 (< 0.01)
Average torque, N.m.						
30 deg/s	107.8±4.1 (24)	139.5±8.8 (12)	31.7 (< 0.005)	118.0±5.0 (25)	143.3±8.2 (12)	25.3 (< 0.02)
180 deg/s	72.5±3.3 (24)	91.1±5.4 (12)	18.6 (< 0.01)	77.9±3.0 (25)	101.3±5.0 (12)	23.4 (< 0.001)
Impulse, N.m.s.						
30 deg/s	290.8±13.6 (24)	400.2±18.3 (12)	109.4 (< 0.001)	317.4±15.5 (25)	406.9±19.8 (12)	89.5 (< 0.005)
180 deg/s	34.9±1.7 (24)	48.6±3.3 (12)	13.7 (< 0.001)	39.0±1.6 (25)	55.1±2.2 (12)	16.1 (< 0.001)

TABLE 40.* Continued.

Elbow extension						
Peak torque, N.m.						
30 deg/s	49.6±1.9 (25)	77.2±4.6 (13)	27.6 (< 0.001)	53.0±2.5 (25)	85.5±4.9 (15)	32.5 (< 0.001)
180 deg/s	38.4±1.3 (25)	60.5±4.0 (13)	22.1 (< 0.001)	43.9±2.6 (25)	72.5±5.0 (15)	28.6 (< 0.001)
Average torque, N.m.						
30 deg/s	39.0±1.7 (25)	60.9±3.8 (13)	21.9 (< 0.001)	39.1±1.8 (25)	65.6±3.3 (15)	26.5 (< 0.001)
180 deg/s	28.9±1.0 (25)	43.5±3.6 (13)	14.6 (< 0.001)	30.7±1.1 (25)	46.9±2.4 (15)	16.2 (< 0.001)
Impulse, N.m.s.						
30 deg/s	148.5±5.7 (25)	205.2±11.4 (13)	56.7 (< 0.001)	151.9±6.2 (25)	222.7±12.1 (15)	70.8 (< 0.001)
180 deg/s	19.7±0.7 (25)	27.1±2.1 (13)	7.4 (< 0.005)	21.3±0.9 (25)	29.7±1.6 (15)	8.4 (< 0.001)

*Left and right values are $\bar{X} \pm$ SE/(N)

Difference values are $\bar{X}$/(p)

TABLE 41. Voluntary strength measurements in weight trainers and control subjects. Values are expressed per kg body mass.

Measure	Left			Right		
	Controls	Weight trainers	Diff.	Controls	Weight trainers	Diff.
Ankle plantar flexion						
Peak torque, N.m/kg						
6 deg/s	3.370±0.140 (24)	3.251±0.315 (11)	0.119 (NS)	3.440±0.130 (25)	3.449±0.235 (12)	0.009 (NS)
36 deg/s	1.775±0.104 (24)	1.760±0.216 (11)	0.015 (NS)	1.851±0.092 (25)	1.870±0.149 (12)	0.019 (NS)
Average torque, N.m/kg						
6 deg/s	2.020±0.110 (24)	1.874±0.212 (11)	0.146 (NS)	1.980±0.090 (25)	1.948±0.158 (12)	0.032 (NS)
36 deg/s	1.003±0.056 (24)	1.000±0.114 (11)	0.003 (NS)	1.027±0.055 (25)	1.048±0.081 (12)	0.021 (NS)
Impulse, N.m.s./kg						
6 deg/s	3.310±0.230 (24)	3.739±0.482 (11)	0.429 (NS)	3.520±0.210 (25)	3.617±0.351 (12)	0.097 (NS)
36 deg/s	0.450±0.035 (24)	0.471±0.078 (11)	0.021 (NS)	0.491±0.037 (25)	0.518±0.053 (12)	0.027 (NS)

TABLE 41. Continued.

Knee extension						
Peak torque, N.m/kg						
30 deg/s	2.626±0.090 (24)	2.732±0.128 (12)	0.106 (NS)	2.843±0.107 (25)	2.867±0.153 (12)	0.024 (NS)
180 deg/s	2.028±0.075 (24)	2.033±0.117 (12)	0.005 (NS)	2.193±0.063 (25)	2.253±0.122 (12)	0.060 (NS)
Average torque, N.m/kg						
30 deg/s	1.523±0.061 (24)	1.631±0.100 (12)	0.108 (NS)	1.663±0.082 (25)	1.688±0.109 (12)	0.025 (NS)
180 deg/s	1.024±0.048 (24)	1.066±0.063 (12)	0.042 (NS)	1.091±0.041 (25)	1.186±0.056 (12)	0.095 (NS)
Impulse, N.m.s./kg						
30 deg/s	4.103±0.206 (24)	4.703±0.225 (12)	0.600 (NS)	4.445±0.222 (25)	4.820±0.301 (12)	0.375 (NS)
180 deg/s	0.491±0.024 (24)	0.537±0.042 (12)	0.046 (NS)	0.547±0.022 (25)	0.647±0.031 (12)	0.100 (< 0.02)
Elbow extension						
Peak torque, N.m./kg						
30 deg/s	0.692±0.023 (25)	0.902±0.048 (13)	0.210 (< 0.001)	0.736±0.028 (25)	0.985±0.051 (15)	0.249 (< 0.001)

TABLE 41. Continued.

180 deg/s	0.537±0.015 (25)	0.708±0.043 (13)	0.171 (< 0.001)	0.610±0.029 (25)	0.834±0.049 (15)	0.224 (< 0.001)
Average torque, N.m./kg						
30 deg/s	0.545±0.023 (25)	0.715±0.041 (13)	0.170 (< 0.005)	0.547±0.023 (25)	0.758±0.024 (15)	0.211 (< 0.001)
180 deg/s	0.404±0.013 (25)	0.510±0.039 (13)	0.106 (< 0.02)	0.431±0.014 (25)	0.540±0.022 (15)	0.109 (< 0.001)
Impulse, N.m.s./kg						
30 deg/s	2.080±0.077 (25)	2.409±0.125 (13)	0.329 (< 0.05)	2.123±0.078 (25)	2.577±0.124 (15)	0.454 (< 0.005)
180 deg/s	0.276±0.008 (25)	0.319±0.023 (13)	0.043 (NS)	0.298±0.010 (25)	0.341±0.014 (15)	0.043 (< 0.02)

Left and right values are $\bar{X} \pm$ SE/(N)

Difference values are $\bar{X}$/(p)

Figure 34. Comparison of weight trainers with control subjects in anthropometric measurements and voluntary strength. Comparison is made by expressing the mean values for the weight trainers as a proportion of the values for control subjects (weight trainers/controls). Top: comparison in limb girth; values for left and right sides have been combined. Bottom: comparison in voluntary strength at slow and fast velocities; values for left and right sides and for peak torque, average torque and impulse have been combined. Values are expressed absolutely (○) and per kg body mass (●).

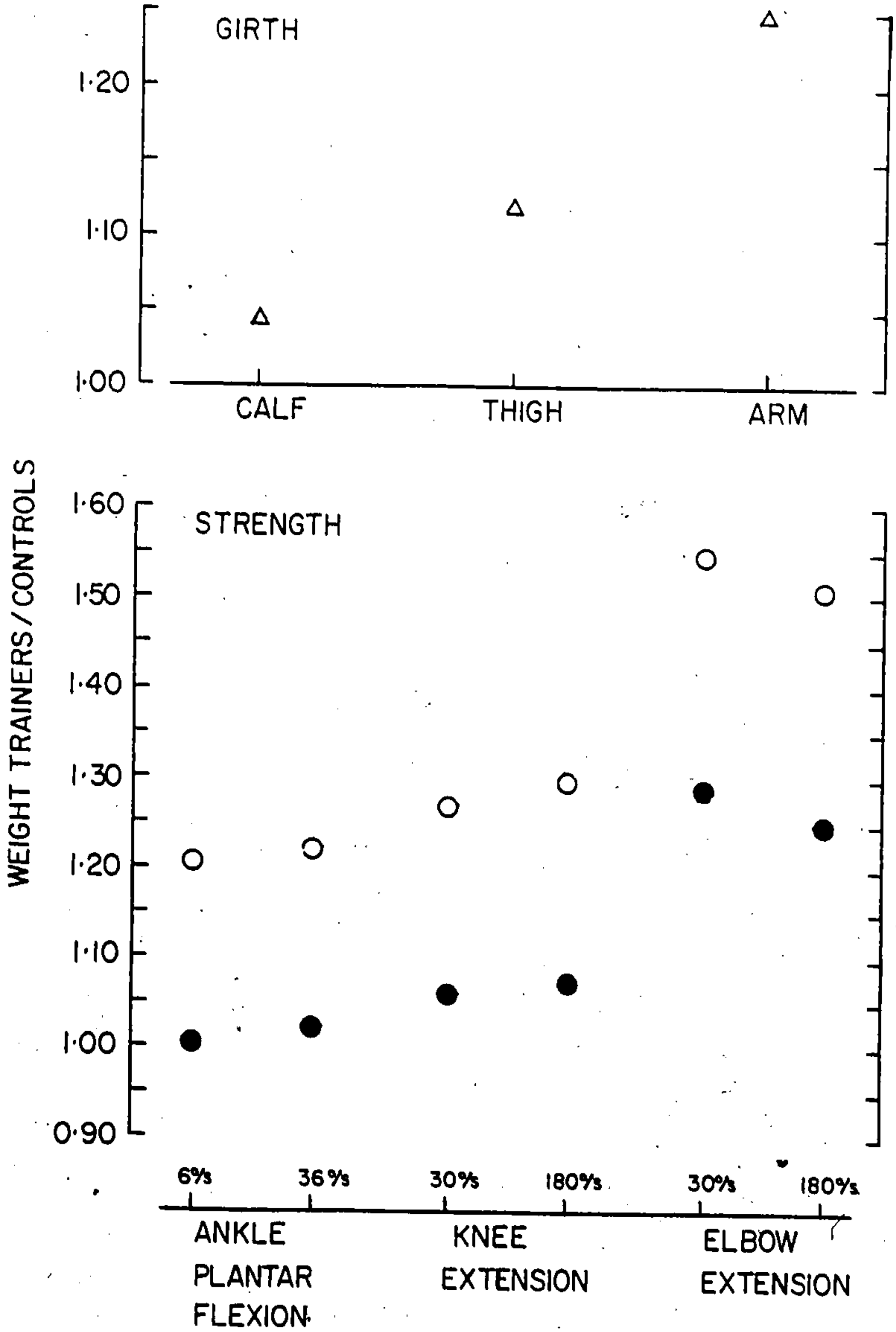

GIRTH
1·20
1·10
1·00
CALF
THIGH
ARM
WEIGHT TRAINERS/CONTROLS
STRENGTH
1·60
1·50
1·40
1·30
1·20
1·10
1·00
0·90
6°/s
36°/s
30°/s
180°/s
30°/s
180°/s
ANKLE PLANTAR FLEXION
KNEE EXTENSION
ELBOW EXTENSION

TABLE 42. Correlations between ankle plantar flexion strength and height, mass, and calf girth in control subjects (N = 24-25) and weight trainers (N = 11-12).

Measure			Height	Mass	Calf girth	
					Left	Right
Peak torque	6 deg/s	left	-0.19	0.25	0.17	0.17
		right	-0.17	0.40**	0.34	0.34
	36 deg/s	left	-0.27	0.17	0.07	0.10
		right	-0.04	0.35*	0.33	0.34
Average torque	6 deg/s	left	-0.09	0.21	-0.01	0.01
		right	0.01	0.38**	0.33	0.30
	36 deg/s	left	-0.15	0.22	0.13	0.17
		right	-0.06	0.36*	0.33	0.33
Impulse	6 deg/s	left	-0.16	0.33	0.22	0.22
		right	-0.14	0.36*	0.31	0.31
	36 deg/s	left	-0.20	0.20	0.12	0.15
		right	-0.07	0.27	0.20	0.20

* $p < 0.05$, ** $p < 0.02$

TABLE 43. Correlations between knee extension strength and height, mass and thigh girth in control subjects (N = 24-25) and weight trainers (N = 12)

Measure			Height	Mass	Thigh girth	
					Left	Right
Peak torque	30 deg/s	left	-0.05	0.50****	0.48****	0.46***
		right	0.21	0.48****	0.43**	0.42**
	180 deg/s	left	0.16	0.43***	0.39*	0.35
		right	0.24	0.58*****	0.46***	0.44**
Average torque	30 deg/s	left	0.09	0.47****	0.39*	0.41*
		right	0.09	0.31	0.33	0.34
	180 deg/s	left	0.05	0.45***	0.46***	0.46***
		right	0.11	0.60*****	0.55***	0.55*****
Impulse	30 deg/s	left	-0.02	0.49****	0.39*	0.38*
		right	-0.07	0.38*	0.27	0.27
	180 deg/s	left	-0.15	0.44***	0.44**	0.44**
		right	-0.14	0.57*****	0.57*****	0.56*****

*$p < 0.05$, **$p < 0.02$, ***$p < 0.01$, ****$p < 0.005$, *****$p < 0.001$

TABLE 44. Correlations between elbow extension strength and height, mass and arm girth in control subjects (N = 25) and weight trainers (N - 13-15).

Measure			Height	Mass	Arm girth	
					Left	Right
Peak torque	30 deg/s	left	-0.12	0.69*	0.82*	0.85*
		right	0.06	0.77*	0.76*	0.82*
	180 deg/s	left	-0.14	0.68*	0.77*	0.78*
		right	0.01	0.74*	0.66*	0.74*
Average torque	30 deg/s	left	-0.16	0.61*	0.72*	0.75*
		right	-0.09	0.69*	0.77*	0.83*
	180 deg/s	left	-0.13	0.47*	0.62*	0.64*
		right	0.01	0.74*	0.66*	0.74*
Impulse	30 deg/s	left	-0.15	0.48*	0.65*	0.67*
		right	0.05	0.66*	0.65*	0.73*
	180 deg/s	left	-0.13	0.55*	0.44*	0.48*
		right	0.15	0.73*	0.62*	0.71*

*$p < 0.001$

weight trainers and controls was reduced (see Figure 34).

The correlations among peak torque, average torque and impulse were positive and high (Table 45); there was a similar high positive correlation between low and high velocity strength (Table 46).

The correlations in strength among ankle plantar flexion, knee extension and elbow extension are presented in Table 47. The correlation was highest between knee extension and elbow extension and lowest between knee extension and ankle plantar flexion. Overall, the significant correlations were low or moderate (r = 0.34-0.70).

The results of the strength-velocity relation determinations in weight trainers and controls are presented in Table 48. There were no significant differences between the two groups in the strength-velocity relation, except in one instance.

The results of the symmetry ratio determinations in weight trainers and controls are presented in Table 49. In low velocity strength, the symmetry ratios in weight trainers were consistently greater than in controls; however, the difference was not significant. There were no significant differences between the two groups in the symmetry ratios of high velocity strength.

3. Electrophysiological Measurements. The results of the electrophysiological measurements in controls and weight trainers are presented in Table 50. There was no significant difference between the two groups in thenar and soleus motor unit counts and M wave amplitude. Reflex potentiation in soleus was significantly greater by 70% in the weight trainers than in the controls. There was no significant difference between the two groups in reflex potentiation in the thenar muscles. Motor nerve conduction velocity of the median nerve was

TABLE 45. Correlations among the mechanical properties of voluntary strength measurements in control subjects ($N = 24\text{-}25$) and weight trainers ($N = 11\text{-}15$).

Movement			Peak torque vs average torque	Peak torque vs impulse	Average torque vs impulse
Ankle plantar flexion	6 deg/s	left	0.91	0.91	0.79
		right	0.89	0.83	0.70
	36 deg/s	left	0.95	0.93	0.94
		right	0.94	0.91	0.89
Knee extension	30 deg/s	left	0.87	0.81	0.85
		right	0.89	0.76	0.79
	180 deg/s	left	0.85	0.72	0.85
		right	0.79	0.60	0.88
Elbow extension	30 deg/s	left	0.96	0.91	0.95
		right	0.88	0.81	0.92
	180 deg/s	left	0.91	0.87	0.94
		right	0.87	0.82	0.88

Note: All correlations are significant at $p < 0.001$

TABLE 46. Correlation between low and high velocity strength in control subjects (N = 24-25) and weight trainers (N = 11-15).

Movement		Low vs High Velocity		
		Peak torque	Average torque	Impulse
Ankle plantar flexion (6 deg/s vs 36 deg/s)	left	0.87	0.87	0.85
	right	0.77	0.81	0.80
Knee extension (30 deg/s vs 180 deg/s)	left	0.70	0.86	0.82
	right	0.70	0.78	0.82
Elbow extension (30 deg/s vs 180 deg/s)	left	0.91	0.93	0.93
	right	0.86	0.91	0.85

Note: All correlations significant at $p < 0.001$

TABLE 47. Correlations among ankle plantar flexion, knee extension and elbow extension in voluntary strength in control subjects (N = 24-25) and weight trainers (N = 11-15)

Measure		Ankle plantar flexion vs Knee extension	Ankle plantar flexion vs Elbow extension	Knee extension vs Elbow extension
Peak torque				
low velocity	left	0.34*	0.45***	0.62*****
	right	0.34*	0.51*****	0.54*****
high velocity	left	0.24	0.45***	0.39**
	right	0.29	0.36*	0.42***
Average torque				
low velocity	left	0.22	0.38*	0.67*****
	right	0.30	0.37*	0.52*****
high velocity	left	0.42**	0.54*****	0.56*****
	right	0.38*	0.38*	0.69*****
Impulse				
low velocity	left	0.35*	0.60*****	0.70*****
	right	0.27	0.37*	0.62*****

TABLE 47. Continued.

high velocity	left	0.49****	0.51****	0.68*****
	right	0.38**	0.32	0.66*****

*p 0.05, **p 0.02, ***p 0.01, ****p 0.005, *****p 0.001

Note: For elbow extension and knee extension, the low and high velocities were 30 deg/s and 180 deg/s respectively. For ankle plantar flexion, the low and high velocities were 6 deg/s and 36 deg/s respectively.

TABLE 48. Strength-velocity relation in weight trainers and control subjects.

Measure		Strength-velocity relation		
		Controls	Weight trainers	Diff.
Ankle plantar flexion (36 deg/s)/(6 deg/s)	Peak torque			
	left	0.525±0.024 (24)	0.533±0.021 (11)	0.008 (NS)
	right	0.541±0.021 (25)	0.543±0.031 (12)	0.002 (NS)
	Average torque			
	left	0.501±0.020 (24)	0.537±0.021 (11)	0.036 (NS)
	right	0.520±0.017 (25)	0.548±0.028 (12)	0.028 (NS)
	Impulse			
	left	0.139±0.008 (24)	0.117±0.009 (11)	0.022 (NS)
	right	0.138±0.008 (25)	0.140±0.011 (12)	0.002 (NS)

TABLE 48. Continued.

Knee extension (180 deg/s)/(30 deg/s)	Peak torque			
	left	0.783±0.027 (24)	0.744±0.026 (12)	0.039 (NS)
	right	0.786±0.024 (25)	0.798±0.035 (12)	0.012 (NS)
	Average torque			
	left	0.672±0.020 (24)	0.656±0.020 (12)	0.016 (NS)
	right	0.672±0.021 (25)	0.715±0.026 (12)	0.043 (NS)
	Impulse			
	left	0.123±0.004 (24)	0.120±0.006 (12)	0.003 (NS)
	right	0.126±0.004 (25)	0.138±0.005 (12)	0.012 (NS)
Elbow extension (180 deg/s)/(30 deg/s)	Peak torque			
	left	0.783±0.018 (25)	0.784±0.027 (13)	0.001 (NS)

TABLE 48. Continued.

right	0.833±0.028 (25)	0.861±0.042 (15)	0.028 (NS)
Average torque			
left	0.755±0.021 (25)	0.706±0.023 (13)	0.049 (NS)
right	0.807±0.029 (25)	0.720±0.021 (15)	0.087 (< 0.025)
Impulse			
left	0.135±0.003 (25)	0.132±0.004 (13)	0.003 (NS)
right	0.142±0.005 (25)	0.133±0.004 (15)	0.009 (NS)

Values for controls and weight trainers are $\bar{X} \pm SE/(N)$

Difference values are $\bar{X}/(p)$

TABLE 49. Symmetry ratios of strength measurements in weight trainers and control subjects.

Measure		Symmetry ratio		
		Controls	Weight trainers	Diff.
Ankle plantar flexion	Peak torque			
	6 deg/s	0.873±0.017 (24)	0.884±0.022 (11)	0.011 (NS)
	36 deg/s	0.830±0.029 (24)	0.858±0.027 (11)	0.028 (NS)
	Average torque			
	6 deg/s	0.855±0.019 (24)	0.872±0.030 (11)	0.017 (NS)
	36 deg/s	0.838±0.025 (24)	0.871±0.019 (11)	0.033 (NS)
	Impulse			
	6 deg/s	0.795±0.025 (24)	0.848±0.053 (11)	0.053 (NS)
	36 deg/s	0.776±0.036 (24)	0.795±0.043 (11)	0.019 (NS)

TABLE 49. Continued.

Knee extension	Peak torque			
	30 deg/s	0.885±0.017 (24)	0.907±0.024 (12)	0.022 (NS)
	180 deg/s	0.888±0.016 (24)	0.880±0.020 (12)	0.008 (NS)
	Average torque			
	30 deg/s	0.880±0.021 (24)	0.928±0.015 (12)	0.048 (NS)
	180 deg/s	0.905±0.014 (24)	0.896±0.025 (12)	-0.009 (NS)
	Impulse			
	30 deg/s	0.890±0.018 (24)	0.904±0.024 (12)	0.014 (NS)
	180 deg/s	0.890±0.015 (24)	0.856±0.032 (12)	0.034 (NS)
Elbow extension	Peak torque			
	30 deg/s	0.878±0.022 (25)	0.924±0.022 (13)	0.046 (NS)
	180 deg/s	0.843±0.026 (25)	0.836±0.032 (13)	0.007 (NS)

TABLE 49. Continued.

Average torque			
30 deg/s	0.885 ± 0.014 (25)	0.915 ± 0.062 (13)	0.030 (NS)
180 deg/s	0.892 ± 0.019 (25)	0.889 ± 0.032 (13)	0.003 (NS)
Impulse			
30 deg/s	0.864 ± 0.017 (25)	0.909 ± 0.020 (13)	0.045 (NS)
180 deg/s	0.889 ± 0.098 (25)	0.860 ± 0.034 (13)	0.029 (NS)

Values for controls and weight trainers are $\bar{X} \pm SE/(N)$

Difference values are $\bar{X}/(p)$

TABLE 50. Electrophysiological measurements in controls and weight trainers.

Measure		Controls	Weight trainers	Diff.
Motor unit counts	Thenar	303±32 (25)	340±63 (13)	37 (NS)
	Soleus	1028±83 (40)	938±139 (15)	90 (NS)
M wave amplitude, mV	Thenar	9.8±0.5 (25)	9.7±0.7 (13)	0.1 (NS)
	Soleus	24.8±1.0 (40)	21.2±1.8 (16)	3.6 (NS)
Reflex potentiation				
V_1/Mx100	Thenar	23.2±2.6 (25)	17.9±2.3 (12)	5.3 (NS)
	Soleus	16.4±2.1 (23)	27.9±4.1 (14)	11.5 (< 0.02)
V_2/Mx100	Thenar	23.8±2.6 (25)	20.4±2.2 (12)	3.4 (NS)
Motor nerve conduction velocity, m/s	Median	58.6±0.5 (30)	63.5±1.3 (10)	4.9 (< 0.005)

TABLE 50. Continued.

Twitch properties				
Twitch tension, N	Thenar	2.39±0.17 (18)	2.69±0.32 (9)	0.30 (NS)
	Triceps surae	93.2±2.8 (48)	108.4±4.5 (16)	15.2 (< 0.01)
Contraction time, ms	Thenar	53.4±1.8 (18)	58.3±3.4 (9)	4.9 (NS)
	Triceps Surae	104.5±2.0 (48)	125.7±5.4 (16)	21.2 (< 0.001)
Half relaxation time, ms	Thenar	49.8±2.0 (18)	58.9±5.5 (9)	9.1 (NS)
	Triceps Surae	84.7±2.1 (48)	93.4±5.6 (16)	8.7 (NS)
Rate of tension development, N/S	Thenar	46.3±4.1 (18)	45.6±4.0 (9.0)	0.7 (NS)
	Triceps surae	900.2±27.0 (48)	881.2±45.5 (16)	19.0 (NS)

Values for controls and weight trainers are $\bar{X} \pm$ SE/(N)

Difference values are $\bar{X}$/(p)

significantly greater by 8% in the weight trainers than in the controls. Twitch tension and contraction time in triceps surae were significantly greater by 16% and 20% respectively in the weight trainers than in the controls. There were no significant differences between the two groups in the twitch properties of the thenar muscles.

E. Electrophysiological Measurements in Gymnasts

1. Motor Units. The motor unit characteristics in the controls and gymnasts are presented in Table 51. In extensor digitorum brevis, thenar and hypothenar muscles, the motor unit counts were significantly less in the gymnasts than in the controls. The mean values for the gymnasts were 65%, 57% and 55% of the control values for extensor digitorum brevis, thenar and hypothenar muscles respectively. There was no significant difference between gymnasts and controls in the number of motor units in brachioradialis and soleus muscles.

The mean motor unit potential amplitude in the hypothenar muscles was 39% ($p<0.05$) greater in the gymnasts than in the controls. In extensor digitorum brevis, thenar, brachioradialis and soleus muscles, there were no significant differences between controls and gymnasts in this measure.

The control value for M wave amplitude in extensor digitorum brevis was 49% ($p<0.02$) greater than the value for the gymnasts. In thenar, hypothenar, brachioradialis and soleus, there were no significant differences between controls and gymnasts in this measure.

In one gymnast, M.P. (male, 21y), it was possible to make measurements on several occasions. Each test on a muscle group was performed on a separate day. The brachioradialis motor unit counts on three

TABLE 51. Motor unit characteristics in controls and gymnasts

Measure		Controls	Gymnasts	Diff.
Motor unit counts				
	Extensor digitorum brevis	200±18 (25)	131±18 (6)	69 (< 0.02)
	Thenar	304±31 (26)	174±47 (6)	130 (< 0.05)
	Hypothenar	504±34 (14)	278±55 (3)	226 (< 0.005)
	Brachioradialis	864±79 (48)	799±37 (4)	65 (NS)
	Soleus	1045±76 (43)	1062±110 (4)	17 (NS)
Mean motor unit potential amplitude, uV				
	Extensor digitorum brevis	44.6±4.0 (25)	44.5±4.9 (6)	0.1 (NS)
	Thenar	38.4±4.1 (26)	48.3±6.7 (6)	9.9 (NS)
	Hypothenar	29.0±2.5 (14)	40.3±4.4 (3)	11.3 (< 0.05)
	Brachioradialis	12.3±0.5 (48)	11.7±0.8 (4)	0.6 (NS)

TABLE 51. Continued.

Soleus	27.2±1.9 (43)	25.2±2.2 (4)	2.0 (NS)
M wave amplitude, mV			
Extensor digitorum brevis	8.4±0.7 (25)	5.7±0.9 (6)	2.8 (< 0.02)
Thenar	9.7±0.5 (26)	7.5±1.3 (6)	2.2 (NS)
Hypothenar	13.9±0.8 (14)	10.9±1.6 (3)	3.0 (NS)
Brachioradialis	9.4±0.5 (48)	9.3±0.8 (4)	0.1 (NS)
Soleus	24.3±0.9 (43)	26.8±3.5 (4)	2.5 (NS)

Values for controls and gymnasts are $\bar{X} \pm SE/(N)$
Difference values are $\bar{X}/(p)$

occasions were 755, 800, and 750 ($\bar{X}\pm$SD, 768±28). The mean value was 0.2 SD below the mean value of the control group. The maximum M wave amplitudes on the three occasions were 7.4, 10.4 and 10.5 mV ($\bar{X}\pm$SD, 9.4±1.8 mV). The mean value was the same as that of the control group. The soleus motor unit counts on two occasions were 890 and 1088 ($\bar{X}\pm$SD, 989±140). The mean value was 0.1 SD below the mean of the control group. The maximum M wave amplitudes on the two occasions were 20.0 and 24.5 mV ($\bar{X}\pm$SD, 22.3±3.2 mV). The mean value was 0.3 SD below the mean of the control group. The number of motor units within the left extensor digitorum brevis was estimated on three occasions. The values were 71, 82 and 71 units ($\bar{X}\pm$SD, 75±6). The mean value was 1.42 SD below the mean of the control group. The values for M wave amplitude were 3.1, 4.2 and 3.7 mV ($\bar{X}\pm$SD, 3.7±0.6 mV). The mean value was 1.5 SD below the mean value for the control group. On the right side, the motor unit counts estimated on two occasions were 100 and 66 ($\bar{X}\pm$SD, 83±24). The mean value was 1.3 SD below the mean for the control group. The maximum M wave amplitudes were 5.8 and 4.8 mV ($\bar{X}\pm$SD, 5.3±0.7 mV). The mean value was 1.0 SD below the mean value for the control group.

The number of motor units within the median innervated thenar muscles of the left side were estimated on three occasions. The values were 123, 152 and 131 units ($\bar{X}\pm$SD, 135±15). The mean value was 1.1 SD below the mean value for the control group. The maximum M wave values were 7.4, 8.2 and 7.2 mV ($\bar{X}\pm$SD, 7.6±0.5 mV). The mean value was 0.8 SD below the mean value for the control group. On the right side, the motor unit counts estmiated on two occasions were 134 and 152 ($\bar{X}\pm$SD, 138±20). The mean value was 1.1 SD below the mean value for the control group. The maximum M wave amplitudes were 7.8 and 7.9 mV. The mean value was 0.7 SD below the mean value for the control group.

The number of motor units within the left hypothenar muscles was estimated on two occasions. The values were 192 and 106 units ($\bar{X}\pm$SD, 149±61). The mean value was 2.8 SD below the mean value for the control group. The maximum M wave values were 9.4 and 11.0 mV ($\bar{X}\pm$SD, 10.2±1.1 mV). The mean value was 1.2 SD below the mean for the control group. On the right side, the motor unit count estimated on one occasion was 172, or 2.6 SD below the mean of the control group. The maximum M wave amplitude was 9.6 mV, or 1.4 SD below the mean value for the control group.

In this subject the median sensory nerve conduction velocity was, for the left side, 58 m/s and for the right side, 64 m/s. The corresponding values for the amplitude of the evoked sensory nerve potentials were 35 and 33 uV respectively. The ulnar sensory nerve conduction velocity for the right side was 55 m/s and the sensory nerve potential amplitude was 12 uV.

The left extensor digitorum brevis of another gymnast (D.G., female, 14 y) was investigated on two separate occasions. The motor unit counts on the two occasions were 147 and 125 ($\bar{X}\pm$SD, 136±15.6). The mean value was 0.7 SD below the mean value for the control group. The maximum M wave amplitudes on the two occasions were 6.3 and 6.4 mV. The mean value was 0.65 SD below the mean value for the control group.

2. Nerve Conduction Velocity. The results of the motor nerve conduction velocity measurements in controls and gymnasts are presented in Table 52. The gymnasts' value for the deep peroneal nerve exceeded that of the controls by 6% ($p < 0.02$). There were no significant differences between the gymnasts and controls in conduction velocity in the median and ulnar nerves.

In three gymnasts, median and ulnar sensory nerve conduction velocity was measured. The mean (±SD) conduction velocity of the median and ulnar nerves was 60.7±3.1 m/s and 58.3±4.9 m/s, respectively. The mean median and ulnar sensory nerve potential amplitude was 30.7±2.1 uV and 11.7±1.5 uV,

TABLE 52. Motor nerve conduction velocity in controls and gymnasts

Nerve	Conduction Velocity, m/s		
	Controls	Gymnasts	Diff.
Deep peroneal nerve	47.5 ± 0.6 (24)	50.5 ± 1.0 (6)	3.0 (< 0.02)
Median	58.9 ± 0.6 (31)	60.0 ± 1.9 (5)	1.1 (NS)
Ulnar	60.2 ± 1.4 (13)	59.0 ± 3.0 (3)	1.2 (NS)

Values for controls and gymnasts are $\bar{X} \pm SE/(N)$

Difference values are $\bar{X}/(p)$

respectively. In the DISCUSSION, these results are related to those obtained in control subjects by McComas et al (1974), using the same method at the same centre.

3. Reflex Potentiation. The results of the reflex potentiation measurements are presented in Table 53. In both brachioradialis and extensor digitorum brevis and in both V_1 and V_2 potentiation, the values for the gymnasts exceeded those of the controls by 37-98%; however, the differences between the two groups were not statistically significant.

4. Muscle Twitch Properties. The muscle twitch properties of triceps surae in gymnasts and controls are presented in Table 54. Contraction time and half relaxation time were significantly greater by 16% and 33% respectively in female controls than in female gymnasts. The average twitch tension of the female control subjects was 21% greater than thatof the female gymnasts; however, the difference was not statistically significant. There were no other significant differences between gymnasts and controls in muscle twitch properties.

F. Knee Extension Strength in Athletes

1. Peak Torque. The results of the peak torque measurements of knee extension in athletes and controls are shown in Figure 35. When values were expressed absolutely, the value ($\bar{x}$±SE, N.m) at 30 deg/s for the left side in the weight lifters (232.6±10.7) exceeded those of the controls (185.8±5.4), sprinters (160.0±1.6), cross-country skiers (163.8±15.8) and the cyclists (187.1±5.5) by 25% ($p<0.001$), 45% ($p<0.001$), 42% ($p<0.005$) and 25% ($p<0.005$) respectively. The cyclists and controls' values exceeded the sprinters' value by 17% ($p<0.005$) and 16% ($p<0.001$) respectively. On the right side, the weight lifters' value (243.4±13.1)

TABLE 53. Reflex potentiation in controls and gymnasts

Measure		Controls	Gymnasts	Diff.
$V_1/Mx100$				
	Brachioradialis	31.5 ± 3.1 (35)	43.0 ± 6.0 (4)	11.5 (NS)
	Extensor digitorum brevis	11.1 ± 1.9 (16)	22.0 ± 6.1 (4)	10.9 (NS)
$V_2/Mx100$				
	Brachioradialis	26.7 ± 2.6 (32)	34.3 ± 7.3 (4)	7.6 (NS)
	Extensor digitorum brevis	18.1 ± 2.3 (16)	26.8 ± 6.1 (4)	8.7 (NS)

Values for controls and gymnasts are $\bar{X} \pm SE/(N)$

Difference values are $\bar{X}/(p)$

TABLE 54. Twitch properties in triceps surae in controls and gymnasts

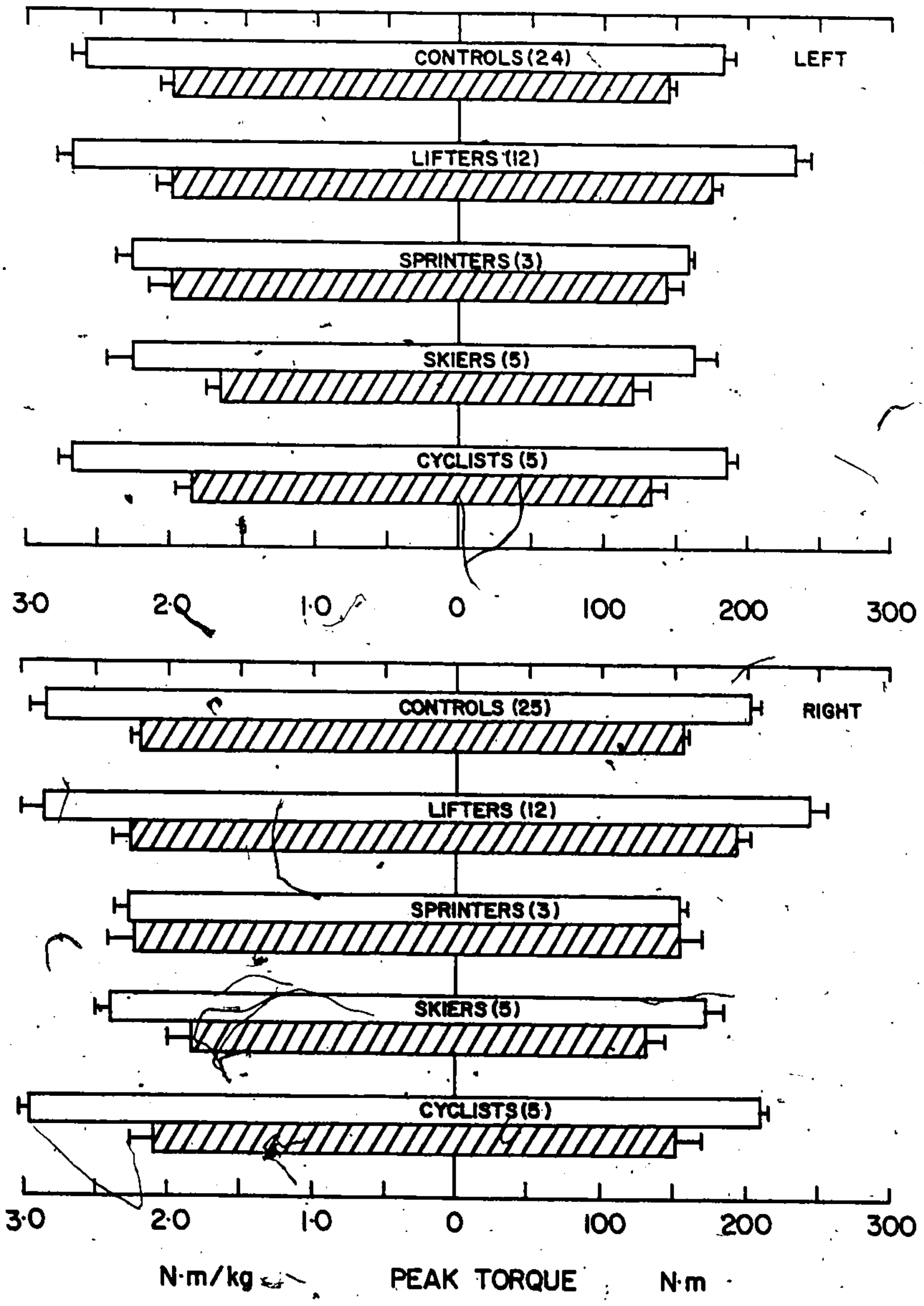
Measure		Controls	Gymnasts	Diff.
Twitch tension, N				
	Females	92.6±3.2 (10)	76.5±12.9 (3)	16.1 (NS)
	Males	93.8±2.8 (46)	89.0±14.0 (3)	4.8 (NS)
Contraction time, ms				
	Females	115.8±3.7 (10)	100.0±4.0 (3)	15.8 (< 0.02)
	Males	104.4±2.1 (46)	97.7±6.2 (3)	6.7 (NS)
Half relaxation time, ms				
	Females	96.6±5.6 (10)	72.7±6.6 (3)	23.9 (< 0.02)
	Males	85.2±2.1 (46)	75.0±5.0 (3)	10.2 (NS)
Rate of tension development, N/S				
	Females	802.2±23.5 (10)	760.0±112.1 (3)	42.2 (NS)

TABLE 54. Continued.

Males	906.1 27.5 (46)	918.6 162.9 (3)	12.5 (NS)

Values for controls and gymnasts are $\bar{X} \pm SE/(N)$
Difference values are $\bar{X}/(p)$

Figure 35. Peak torque of left (top) and right (bottom) knee extension at 30°/s (open bars) and 180°/s (hatched bars) in control subjects (N = 24-25) and in weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5). Values ($\bar{X}$ and SE) are expressed absolutely and per kg body mass.


CONTROLS (24)
LEFT
LIFTERS (12)
SPRINTERS (3)
SKIERS (5)
CYCLISTS (5)
3·0
2·0
1·0
0
100
200
300
CONTROLS (25)
RIGHT
LIFTERS (12)
SPRINTERS (3)
SKIERS (5)
CYCLISTS (5)
3·0
2·0
1·0
0
100
200
300
N·m/kg
PEAK TORQUE
N·m

exceeded those of the controls (202.5±7.2), sprinters (158.2±1.8), cross country skiers (172.5±11.2) and cyclists (210.2±7.1) by 20% ($p<0.02$), 54% ($p<0.001$), 41% ($p<0.001$) and 16% ($p<0.05$) respectively. The cyclists' value exceeded those of the sprinters and cross country skiers by 33% ($p<0.001$) and 22% ($p<0.025$) respectively. The controls' value exceeded those of the sprinters and cross country skiers by 28% ($p<0.001$) and 17% ($p<0.05$) respectively.

At 180 deg/s on the left side, the weight lifters' value (172.7±9.3) exceeded those of the controls (144.1±5.2), cross country skiers (120.4±12.7) and cyclists (131.5±13.8) by 20% ($p<0.02$), 43% ($p<0.005$) and 31% ($p<0.05$) respectively. On the right side, the weight lifters' value (192.5±11.4) exceeded those of the controls (156.6±4.9) and cross country skiers (131.3±16.0) by 23% ($p<0.01$) and 47% ($p<0.01$) respectively.

When the results of the peak torque measurements were expressed per kg body mass, the values ($\bar{x}$±SE, N.m/kg) at 30 deg/s for the left side in weight lifters (2.73±0.12) and controls (2.63±0.09) exceeded the sprinters' value (2.30±0.10) by 19% ($p<0.025$) and 14% ($p<0.025$) respectively. On the right side, the cyclists' value (2.99±0.15) exceeded those of the sprinters (2.27±0.08) and cross country skiers (2.40±0.10) by 32% ($p<0.01$) and 25% ($p<0.02$) respectively. The weight lifters' value (2.85±0.15) exceeded those of the sprinters and cross country skiers by 26% ($p<0.01$) and 19% ($p<0.025$) respectively. The controls' value (2.84±0.11) exceeded those of the sprinters and cross country skiers by 25% ($p<0.001$) and 18% ($p<0.01$) respectively.

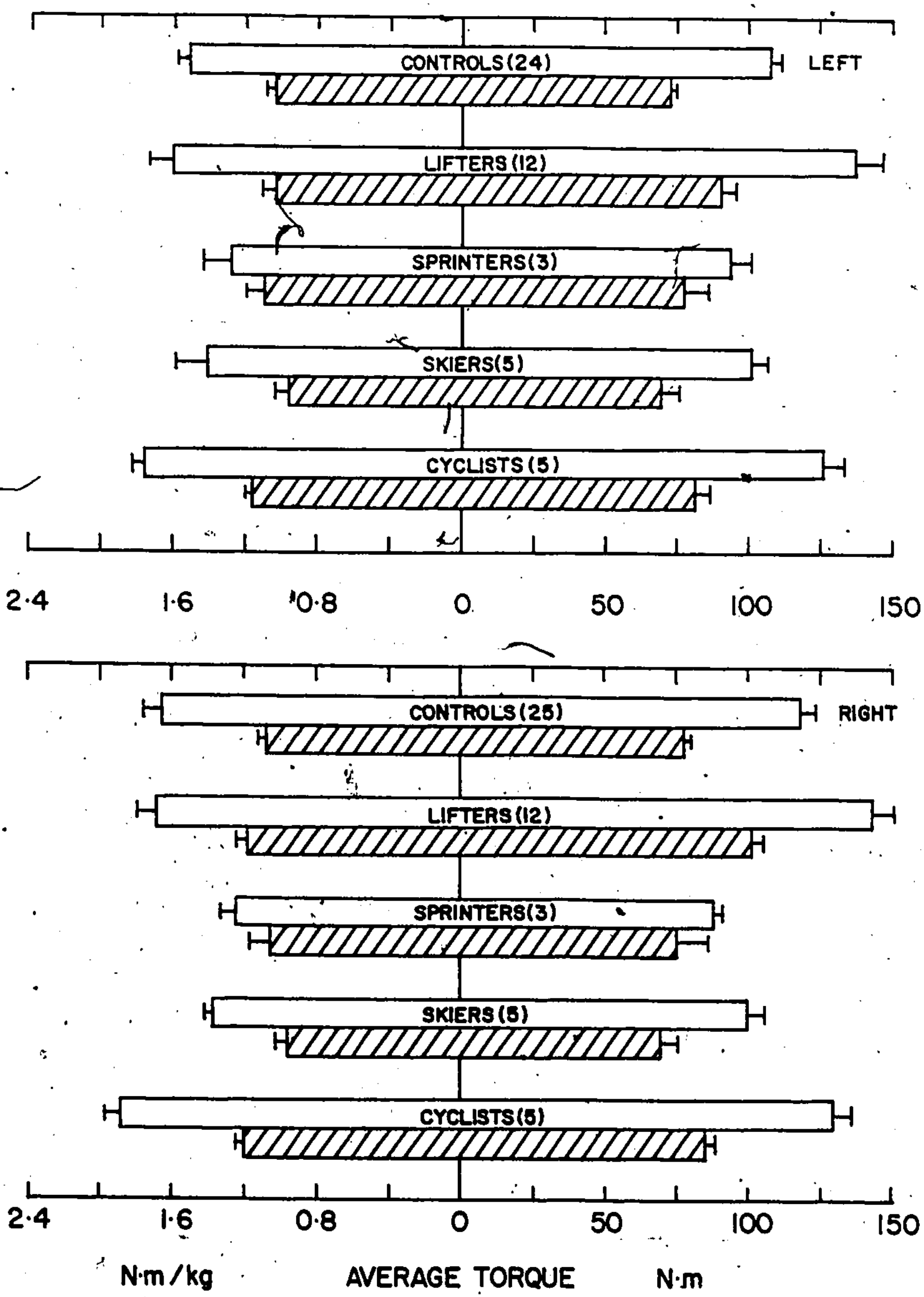
At 180 deg/s on the left side, the values for the controls (2.03±0.05) and weight lifters (2.03±0.12) exceeded the cross country skiers' value (1.66±0.11) by 22% (p<0.005) and 22% (p<0.05) respectively. On the right side, there were no significant differences among the groups.

2) Average Torque. The results of the average torque measurements are shown in Figure 36. When the values were expressed absolutely, the value (x̄±SE, N.m) at 30 deg/s on the left side in the weight lifters (139.5±8.8) exceeded those of the controls (107.8±4.1), sprinters (94.4±7.0) and cross country skiers (102.7±11.6) by 29% (p<0.005), 48% (p<0.005) and 36% (p<0.025) respectively. The cyclists' value (125.8±8.6) exceeded the sprinters' value by 33% (p<0.05). On the right side, the weight lifters' value (143.3±8.2) exceeded those of the controls (118.0±5.0), sprinters (87.1±5.1) and cross country skiers (99.5±7.2) by 29% (p<0.005), 48% (p<0.005) and 36% (p<0.025) respectively. The cyclists' value (129.3±8.0) exceeded those of the sprinters and cross country skiers by 48% (p<0.005) and 30% (p<0.025) respectively. The controls' value exceeded those of the sprinters and cross country skiers by 36% (p<0.001) and 19% (p<0.05) respectively.

At 180 deg/s on the left side, the weight lifters' value (91.1±5.4) exceeded those of the controls (72.5±3.3) and cross country skiers (69.5±8.1) by 26% (p<0.01) and 31% (p<0.05) respectively. On the right side, the weight lifters' value (101.3±5.0) exceeded those of the controls (77.9±3.0), cross country skiers (69.2±6.7) and cyclists (85.0±3.6) by 30% (p<0.001), 46% (p<0.005) and 19% (p<0.02) respectively.

When the results of the average torque measurements were expressed per kg body mass, the value (x̄±SE, N.m/kg) at 30 deg/s on the left side in the cyclists (1.77±0.05) exceeded those of the controls

Figure 36. Average torque of left (top) and right (bottom) knee extension at 30 deg/s (open bars) and 180 deg/s (hatched bars) in control subjects (N = 24-25) and in weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5). Values ($\bar{X}$ and SE) are expressed absolutely and per kg body mass.

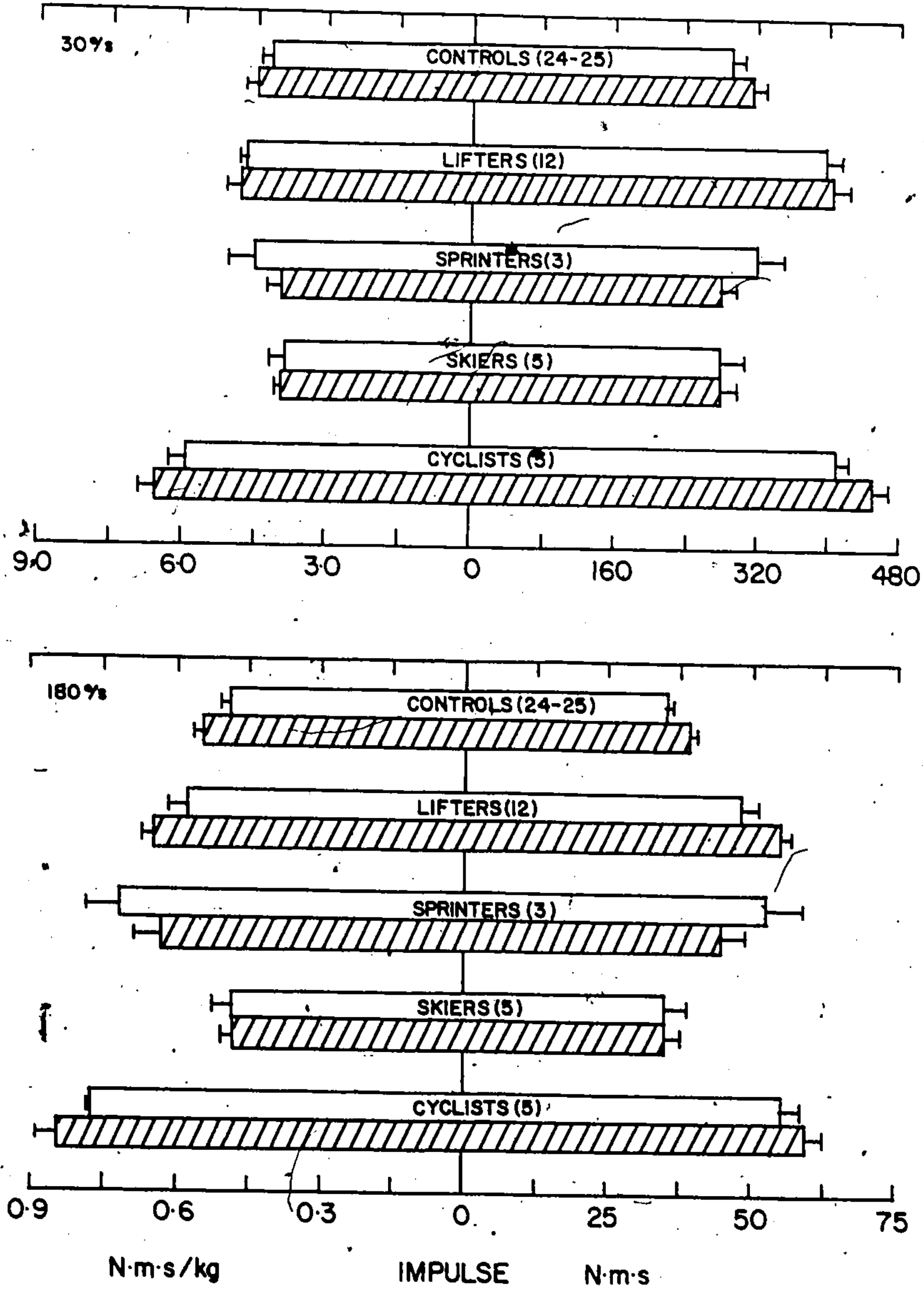

CONTROLS(24)
LEFT
LIFTERS(12)
SPRINTERS(3)
SKIERS(5)
CYCLISTS(5)
2·4
1·6
0·8
0
50
100
150
CONTROLS(25)
RIGHT
LIFTERS(12)
SPRINTERS(3)
SKIERS(5)
CYCLISTS(5)
2·4
1·6
0·8
0
50
100
150
N·m/kg
AVERAGE TORQUE
N·m

(1.52±0.06) and sprinters (1.35±0.11) by 16% ($p<0.005$) and 31% ($p<0.025$) respectively. On the right side, the cyclists' value (1.83±0.09) exceeded those of the sprinters (1.25±0.07) and cross country skiers (1.38±0.04) by 46% ($p<0.005$) and 33% ($p<0.005$) respectively. The weight lifters' value (1.69±0.11) exceeded those of the sprinters and cross country skiers by 35% ($p<0.01$) and 22% ($p<0.02$) respectively. The controls' value (1.66±0.08) exceeded those of the sprinters and cross country skiers by 33% ($p<0.001$) and 20% ($p<0.005$) respectively.

At 180 deg/s on the left side, the cyclists' value (1.16±0.02) exceeded those of the controls (1.02±0.05) and cross country skiers (0.96±0.08) by 14% ($p<0.02$) and 21% ($p<0.05$) respectively. On the right side, the values for the cyclists (1.21±0.05) and the weight lifters (1.16±0.06) exceeded that of the cross country skiers (0.96±0.07) by 26% ($p<0.02$) and 21% ($p<0.05$) respectively.

3. Impulse. The results of the impulse measurements are shown in Figure 37. When the values were expressed absolutely, the value ($\bar{x}$±SE, N.m.s) at 30 deg/s on the left side in the cyclists (414.4±15.6) exceeded those of the controls (290.8±13.6) and cross country skiers (283.5±29.6) by 43% ($p<0.001$) and 46% ($p<0.005$) respectively. The weight lifters' value (400.2±18.3) exceeded those of the controls and cross country skiers by 38% ($p<0.001$) and 41% ($p<0.005$) respectively. On the right side, the cyclists' value (456.7±17.7) exceeded those of the controls (317.4±15.5), sprinters (281.3±21.4) and cross country skiers (281.2±21.5) by 44% ($p<0.001$), 62% ($p<0.005$) and 62% ($p<0.001$) respectively. The weight lifters' value (406.9±19.8) exceeded those of the controls, sprinters and cross country skiers by 28% ($p<0.005$), 45%

Figure 37. Impulse of left (open bars) and right (hatched bars) knee extension at 30 deg/s (top) and 180 deg/s (bottom) in control subjects (N [illegible] 24-25), weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5). Values ($\bar{X}$ and SE) are expressed absolutely and per kg body mass.


30°/s
CONTROLS (24-25)
LIFTERS (12)
SPRINTERS (3)
SKIERS (5)
CYCLISTS (5)
9.0
6.0
3.0
0
160
320
480
180°/s
CONTROLS (24-25)
LIFTERS (12)
SPRINTERS (3)
SKIERS (5)
CYCLISTS (5)
0.9
0.6
0.3
0
25
50
75
N·m·s/kg
IMPULSE
N·m·s

($p<0.001$) and 45% ($p<0.001$) respectively.

At 180 deg/s on the left side, the cyclists' value (55.4±4.0) exceeded those of the controls (34.9±1.7) and cross country skiers (35.0±4.2) by 59% ($p<0.001$) and 58% ($p<0.01$) respectively. The sprinters' value (52.4±6.8) exceeded the controls' value by 50% ($p<0.02$). The weight lifters' value (48.6±3.3) exceeded those of the controls and cross country skiers by 39% ($p<0.001$) and 39% ($p<0.025$) respectively. On the right side, the cyclists' value (59.9±3.1) exceeded those of the controls (39.0±1.6), sprinters (44.0±5.0) and cross country skiers (35.1±2.8) by 53% ($p<0.001$) 36% ($p<0.05$) and 70% ($p<0.005$) respectively. The weight lifters' value (55.1±2.2) exceeded those of the controls and cross country skiers by 41% ($p<0.001$) and 57% ($p<0.001$) respectively.

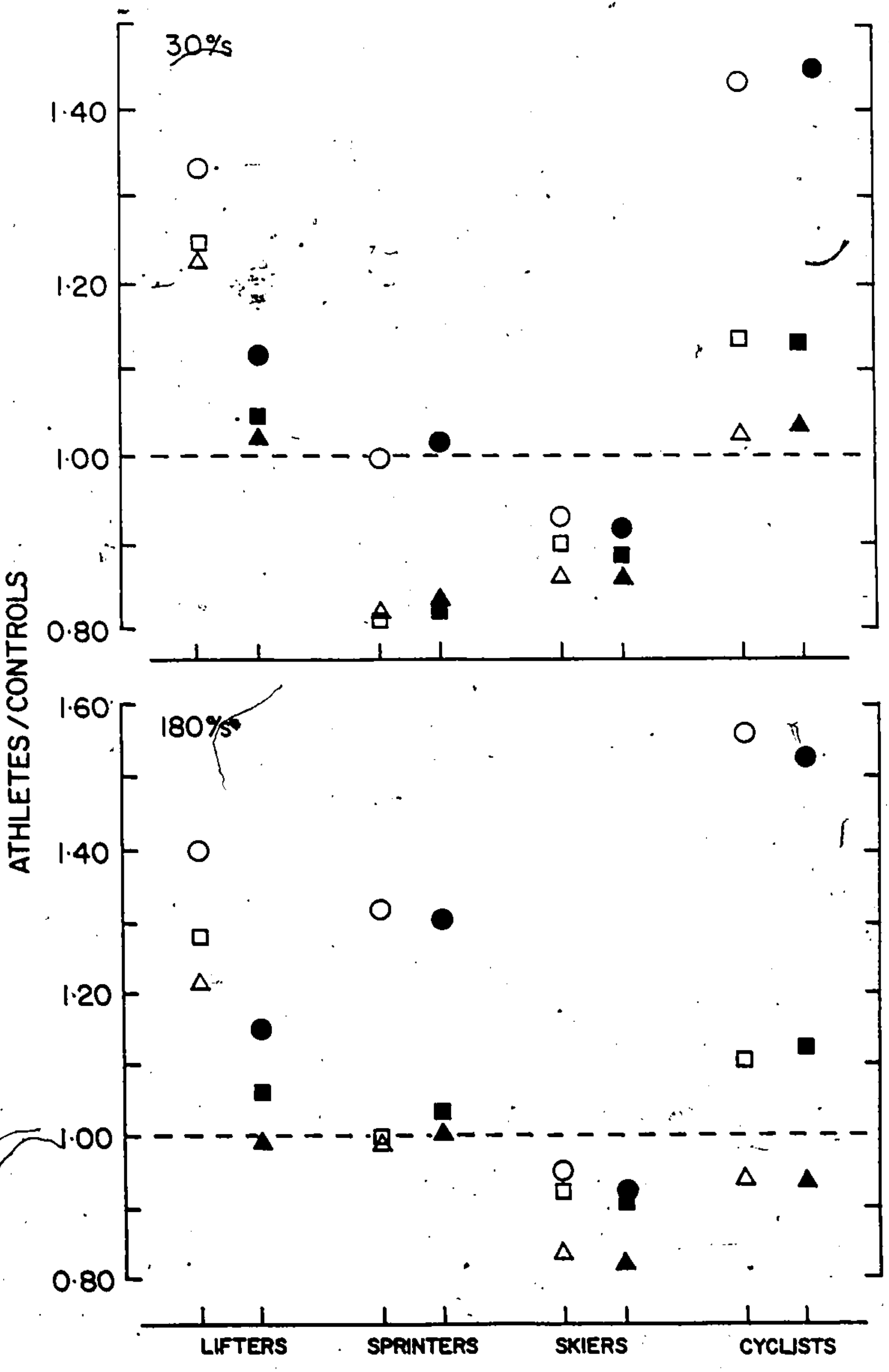
When the results of the impulse measurements were expressed per kg body mass, the value ($\bar{x}$±SE, N.m.s/kg) at 30 deg/s on the left side for the cyclists (5.90±0.31) exceeded those of the controls (4.10±0.21), weight lifters (4.7±0.22) and cross country skiers (3.93±0.30) by 44% ($p<0.001$), 26% ($p<0.01$) and 50% ($p<0.005$) respectively. On the right side, the cyclists' value (6.51±0.44) exceeded those of the controls (4.45±0.22), weight lifters (4.82±0.30), sprinters (4.04±0.36) and cross country skiers (3.80±0.16) by 46% ($p<0.001$), 35% ($p<0.005$), 61% ($p<0.005$), and 67% ($p<0.001$) respectively. The weight lifters' and controls' values exceeded that of the cross country skiers by 24% ($p<0.02$) and 14% ($p<0.025$) respectively.

At 180 deg/s on the left side, the cyclists' value (0.778±0.004) exceeded those of the controls (0.491±0.024), weight lifters (0.573±0.042) and cross country skiers (0.484±0.041) by 58% ($p<0.001$), 36% ($p<0.001$)

and 61% ($p<0.001$) respectively. The sprinters' value (0.747±0.073) exceeded those of the controls and cross country skiers by 52% ($p<0.005$) and 54% ($p<0.025$) respectively. On the right side, the cyclists' value (0.852±0.046) exceeded those of the controls (0.574±0.022), weight lifters (0.647±0.031), sprinters (0.627±0.058) and cross country skiers (0.488±0.024) by 48% ($p<0.001$), 32% ($p<0.005$), 36% ($p<0.025$) and 75% ($p<0.001$) respectively. The weight lifters' and controls' values exceeded the cross country skiers' value by 33% ($p<0.005$) and 18% ($p<0.002$) respectively.

4. <u>Strength in Athletes as a Proportion of Strength in Control Subjects</u>. In Figure 38, the knee extension strength in the groups of athletes has been expressed as a proportion (athletic group value/control value) of the strength in controls subjects. All groups of athletes performed best in relation to control values in impulse and worst in peak torque. Overall, the athlete values for peak torque, average torque and impulse were 97%, 103% and 121% respectively of the corresponding control values. The difference in performance between peak torque and impulse was greatest in the cyclists and sprinters. The cyclists' values for peak torque and impulse were 98% and 149% respectively of the control values. The sprinters' values for peak torque and impulse were 91% and 116% respectively of the control values. The difference in performance between peak torque and impulse was least in the weight lifters and cross country skiers. The weight lifters' values for peak torque and impulse were 112% and 125% respectively of the control values. The cross country skiers' values for peak torque and impulse were 85% and 93% respectively of the control values.

Figure 38. Knee extension strength in weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5) expressed as a proportion of the strength of control subjects (N = 24-25). Values for peak torque (△ ▲), average torque (□ ■) and impulse (○ ●) are presented both absolutely (open symbols) and per kg body mass (filled symbols). Top: strength measured at 30 deg/s. Bottom: strength measured at 180 deg/s. Values for left and right sides have been averaged.


30°/s
180°/s
ATHLETES / CONTROLS
1·40
1·20
1·00
0·80
1·60
LIFTERS
SPRINTERS
SKIERS
CYCLISTS

The performance of the cyclists, sprinters, and cross country skiers in relation to control values was similar whether strength was expressed absolutely or per kg body mass. However, the weight lifters' performance, in relation to control values, was lower when strength was expressed per kg body mass rather than absolutely. The weight lifters' values for strength expressed absolutely and per kg·body mass were 128% and 107% respectively of the control values.

The performance of the weight lifters, cyclists and cross country skiers in relation to control values was similar for both low (30 deg/s) and high (180 deg/s) velocity strength. However, the performance of the sprinters was higher in relation to control values in high velocity strength than in low velocity strength. The sprinters' values for low and high velocity strength were 88% and 111% respectively of the control values. The sprinters' values for low and high velocity impulse were 101% and 131% respectively of the control values.

In peak torque and average torque expressed absolutely, the weight lifters' values were greater in relation to the control values than were the cyclists' values; however, the cyclists' values for impulse exceeded the control value to a greater extent than did the weight lifters' value.

5. <u>Body Mass and Knee Extension Strength</u>. The body mass ($\bar{x}$±SE, kg) of the weight lifters (85.8±3.0) was greater than that of the controls (71.7±1.5, $p<0.001$), sprinters (69.9±2.9, $p<0.005$), cross country skiers (71.7±3.2, $p<0.01$) and the cyclists (71.2±5.0, $p<0.025$). The correlation between body mass and knee extension strength expressed absolutely in the athletes and control subjects is presented in Table 55.

TABLE 55. Correlation between body mass and knee extension strength in controls (N = 24-25), weight lifters (N = 12), sprinters (N - 37), cross country skiers (N = %) and cyclists (N = 5)

Measure			r	p
Peak torque	30 deg/s	left	0.51	< 0.001
		right	0.51	< 0.001
	180 deg/s	left	0.52	< 0.001
		right	0.63	< 0.001
Average torque	30 deg/s	left	0.49	< 0.001
		right	0.38	< 0.005
	180 deg/s	left	0.49	< 0.001
		right	0.62	< 0.001
Impulse	30 deg/s	left	0.41	< 0.005
		right	0.31	< 0.05
	180 deg/s	left	0.35	< 0.02
		right	0.47	< 0.001

There was a significant positive correlation between every measure of absolute strength and body mass; however, the correlations were low to moderate (r = 0.31-0.63).

6. Correlations among Peak Torque, Average Torque and Impulse. The correlations among peak torque, average torque and impulse are presented in Table 56. All correlations were positive and significant and ranged from r = 0.53 to r = 0.90. The lowest correlations were between peak torque and impulse at 180 deg/s. This low correlation is also evident in Figure 38, in which the cyclists and sprinters have relatively low values for peak torque, but relatively high values for impulse. The highest correlations were between peak torque and average torque at 30 deg/s. This high correlation is also evident in Figure 38.

7. Correlation between Low and High Velocity Knee Extension Strength. The correlation between low (30 deg/s) and high (180 deg/s) velocity knee extension strength is presented in Table 57. All correlations were positive and significant. The correlations with respect to peak torque were lower than with respect to average torque and impulse.

8. Correlation between Left and Right Knee Extension Strength. The correlation between left and right extension strength is presented in Table 58. The correlations were high, positive and significant. The correlations were higher at 180 deg/s than at 30 deg/s.

9. Strength-Velocity Relation. The strength-velocity relation ratios of knee extension are shown in Figure 39. In all groups, the strength-velocity relation ratios were highest for peak torque and lowest for impulse. In all measures, the values for the sprinters exceeded those of

TABLE 56. Correlations among peak torque, average torque and impulse of knee extension in controls (N = 24-25), weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5).

Measure		Peak torque vs average torque	Peak torque vs impulse	Average torque vs impulse
30 deg/s	left	0.86	0.70	0.81
	right	0.90	0.70	0.77
180 deg/s	left	0.82	0.57	0.80
	right	0.78	0.53	0.80

Note: all correlations significant at $p < 0.001$

TABLE 57. Correlation between low (30 deg/s) and high (180 deg/s) velocity knee extension strength in controls (N = 24-25), weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5)

Measure	Left	Right
Peak torque	0.68	0.66
Average torque	0.82	0.77
Impulse	0.79	0.84

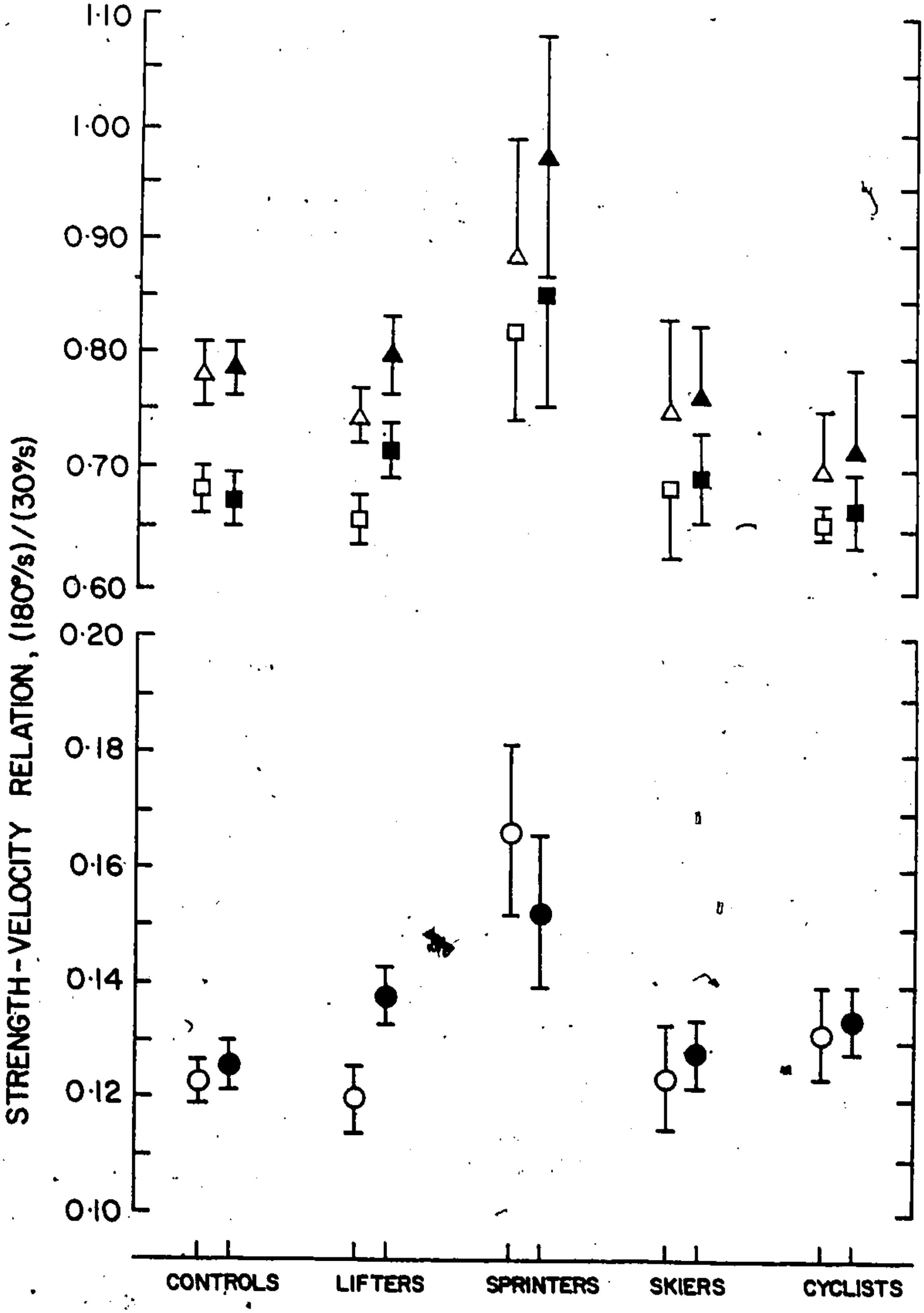
Note: all correlations significant at $p < 0.001$

TABLE 58. Correlation between left and right knee extension strength in controls (N = 24-25), weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5).

Measure	30 deg/s	180 deg/s
Peak torque	0.81	0.85
Average torque	0.78	0.91
Impulse	0.83	0.87

Note: all correlations significant at $p \leq 0.001$

Figure 39. The strength-velocity relation of knee extension in controls (C, N = 24-25) weight lifters (WL, N = 12), sprinters (SP, N = 3), cross country skiers (SK, N = 5) and cyclists (CY, N = 5). Values for left (unfilled symbols) and right (filled symbols) sides are given for peak torque (△ ▲), average torque (□ ■) and impulse (○ ●). Values are $\bar{X} \pm$ SE.


STRENGTH-VELOCITY RELATION, (180°/s)/(30°/s)
1·10
1·00
0·90
0·80
0·70
0·60
0·20
0·18
0·16
0·14
0·12
0·10
CONTROLS
LIFTERS
SPRINTERS
SKIERS
CYCLISTS

the other groups; however, only in impulse on the left side was the value ($\bar{x}$±SE) of the sprinters (0.167±0.015) significantly greater than those of other groups, exceeding the values of the controls (0.123±0.004), weight lifters (0.120±0.006) and cross country skiers (0.124±0.009) by 36% ($p<0.01$), 39% ($p<0.02$) and 35% ($p<0.05$) respectively.

The correlations among peak torque, average torque and impulse in the strength-velocity relation are presented in Table 59. All correlations were positive and significant, but only moderately high. The correlations between left and right sides in the strength-velocity relation were for peak torque, $r = 0.59$, ($p<0.001$); average torque, $r = 0.43$ ($p<0.005$) and for impulse, $r = 0.46$ ($p<0.001$).

10. Symmetry Ratios. The symmetry ratios of knee extension are presented in Table 60. The overall symmetry ratio was approximately 0.9. There were no significant differences among the groups in symmetry ratios. The symmetry ratios did not vary significantly with respect to mechanical property or velocity.

TABLE 59. Correlations among peak torque, average torque and impulse in the strength-velocity relation in knee extension in controls (N = 24-25), weight lifters (N = 12), sprinters (N = 3), cross country skiers (N = 5) and cyclists (N = 5)

Measure	Peak torque vs average torque	Peak torque vs impulse	Average torque vs impulse
left	0.53	0.55	0.68
right	0.56	0.58	0.67

Note: all correlations significant at $p < 0.001$

TABLE 60. Symmetry ratios of knee extension in control subjects and athletes.

Measure		Symmetry ratio				
		Controls (N=24)	Weight lifters (N=12)	Sprinters (N=3)	Cross country skiers (N=5)	Cyclists (N=5)
Peak torque	30 deg/s	0.86±0.09 (0.68-1.00)	0.91±0.09 (0.78-1.00)	0.92±0.08 (0.83-0.98)	0.92±0.06 (0.85-1.00)	0.89±0.11 (0.88-0.90)
	180 deg/s	0.89±0.08 (0.77-1.00)	0.88±0.07 (0.73-0.98)	0.99±0.01 (0.98-1.00)	0.86±0.05 (0.93-0.94)	0.88±0.10 (0.76-1.00)
Average torque	30 deg/s	0.88±0.10 (0.59-1.00)	0.93±0.05 (0.85-0.99)	0.94±0.04 (0.91-0.98)	0.86±0.11 (0.68-0.96)	0.92±0.06 (0.85-1.00)
	180 deg/s	0.91±0.07 (0.67-1.00)	0.90±0.09 (0.69-1.00)	0.93±0.04 (0.88-0.95)	0.95±0.05 (0.88-1.00)	0.92±0.04 (0.89-0.99)
Impulse	30 deg/s	0.89±0.09 (0.64-0.99)	0.90±0.08 (-.71-0.97)	0.84±0.05 (0.80-0.89)	0.89±0.05 (0.82-0.92)	0.91±0.06 (0.85-0.98)
	180 deg/s	0.89±0.08 (0.67-1.00)	0.86±0.11 (0.61-0.95)	0.89±0.07 (0.83-0.97)	0.91±0.06 (0.82-0.97)	0.88±0.07 (0.83-0.99)

Values are $\bar{X} \pm$ SD/(min-max)

IV. DISCUSSION

A. Reproducibility of Measurements

1. Voluntary Strength. The method error for the measurement of peak torque of knee extension on the Cybex was similar to that reported by Thorstensson (1976). For duplicate determinations made on separate days, a method error for the measurement of average torque and impulse of knee extension on the Cybex has not been reported in the literature. In the present investigation, the method error for the measurement of average torque and impulse was similar to that for peak torque. The method error for the measurement of peak torque, average torque and impulse of elbow extension and ankle plantar flexion on the Cybex has not been reported in the literature; in the present investigation, the method error was similar to that for corresponding measurements of knee extension.

The method error for the determination of the strength-velocity relation ratios and the symmetry ratios has not been previously reported; in the present investigation, the method error for these determinations was similar to that for the measurement of the mechanical properties.

The method error for the measurement of voluntary isometric strength of thumb abduction was similar to that reported previously for isometric strength testing (Astrand and Rodahl, 1977, p. 107; Friman, 1977; Simonson, 1971, p 244; Tornvall, 1963). The method error in the measurement of voluntary strength includes both a methodological and biological variation; in the latter, the major factor is the degree of co-operation and motivation expressed by the subject during the testing. To minimize this variation, all subjects received similar instructions and encouragement during testing.

2. Motor Unit Counts. The method error for the motor unit counts, determined from 98 duplicate determinations in 98 subjects involving 5 muscles ranged from 22.0-39.6%. The method error for M wave amplitude, determined in a similar manner, ranged from 3.6-19.2%. The smaller method error for the measurement of M wave amplitude than for motor unit counting has also been found by Sica and McComas (unpublished observations). McComas et al (1971) performed duplicate determinations in six subjects of motor unit counts in extensor digitorum brevis. On the average, the greater of the two determinations exceeded the lesser determination by 33.7% (SD, 31%); this value was similar to the method error for extensor digitorum brevis in the present investigation (39.6%). When several determinations are made in one or two subjects, the day to day variation, as indicated by the coefficient of variation, is smaller. Thus, McComas et al (1971) obtained a coefficient of variation of 13.8% for 11 determinations (on separate days) in one subject for extensor digitorum brevis. Sica et al (1974) obtained coefficients of variation of 10.8% and 9.5% for thenar and hypothenar motor units respectively. For each muscle one subject was investigated on 10 different days. Sica and McComas (unpublished observations) performed motor unit counts on 10 different days in two subjects for various muscles. The coefficients of variation in the two subjects were for extensor digitorum brevis, 12.7% and 10.2%; for median innervated thenar muscles, 12.9% and 12.6%; for hypothenar muscles, 8.0% and 12.7% and for soleus, 9.5% and 7.1%.

In the present investigation, motor unit counts in brachioradialis were determined in seven subjects on several occasions. The coefficients of variation ranged from 11.1% to 34.0%. In soleus in two subjects, the coefficients of variation were 30.6% and 5.3%. These results suggest that when this method is used to determine reproducibility, the procedure should be performed on at least several subjects.

The greater method error for the motor unit counting in relation to that for M wave amplitude is not surprising, because the method for determining the latter is much simpler and there are fewer possibilities for measurement error. The rather large method error for motor unit counting found in the present investigation may in part be due to the fact that a motor unit count is based on the results obtained from a very small sample (8-12 units) of motor units from the total population (Sica et al, 1974). Further, the method error of the M wave measurement contributes to the method error of the motor unit counting.

3. Motor Nerve Conduction Velocity. The reproducibility of this measurement was similar to that reported in the literature (Honet et al, 1968; Norris et al, 1953). Nerve conduction velocity is affected by temperature. Motor conduction velocity has been shown to decrease by 2.4 m/s per degree Celsius fall in intramuscular temperature and by 1.2 m/s per degree Celsius fall in skin temperature (LeQuesne, 1971). Thus, a variation of 3 degrees Celsius

in skin and muscle temperature would cause a variation in conduction velocity of 3.6 m/s and 7.2 m/s respectively. In the present investigation, an attempt was made to control temperature by warming the skin to a temperature between 36-38°C. The method error for the measurement of motor nerve conduction velocity in the present investigation ranged from 0.8-2.7 m/s in the nerves investigated. Possible contributors to the method error included variation in temperature, error in reading latencies and error in measuring distances. The observed small method errors suggest that the method for controlling temperature was successful.

4. Reflex Potentiation. The reproducibility of this measurement has not been reported in the literature. In the present investigation, the method error was fairly large (27%). The method error included a day to day biological variation similar to that discussed in relation to the measurement of voluntary strength. The methodological contribution to the method error was variation in the timing of the supramaximal stimulus to the nerve during the isometric muscle contraction. To minimize the effect of this variation, the mean of ten consecutive trials was taken as the measurement of reflex potentiation. Nevertheless, the method error remained rather large, and a large day to day variation in this measurement must be accepted as a normal finding.

5. Muscle Twitch Properties. The method error in the measurement of muscle twitch properties was notably lower in triceps surae than in extensor hallucis brevis, median innervated thenar muscles and hypothenar muscles. In extensor hallucis brevis, thenar and hypothenar muscles, the testing protocol included subjecting the muscles to an initial tension of 9.81 N. This procedure, which was not done in the case of triceps surae, may have contributed to the method error, and would thus account for the larger method error in the other muscles.

Lambert et al (1951) reported that the mean day to day variation in the duration of the triceps surae twitch was 8%. This finding is similar to that found in the present investigation for contraction time and half relaxation time. There have been no other reports of the reproducibility of muscle twitch measurements in man.

In contrast to the measurement of voluntary strength, variation in motivation did not contribute to the method error in the measurement of peak twitch tension. This difference may explain the greater method error in the measurement of peak torque of voluntary ankle plantar flexion (11.5%) than in the measurement of the peak twitch tension of triceps surae (5.6%).

6. Anthropometric Measurements. The method error in the anthropometric measurements (body mass, limb girth) was very small in comparison to those of the other measurements. The simplicity of the anthropometric measurements reduced the possible extent of methodological variation, and the relative role of biological variation was, for these measurements, very small.

B. Control Measurements

1. Voluntary Strength and Anthropometric Measurements.

The results of the measurement of peak torque of knee extension at 30 deg/s on the Cybex are similar to those found by Fahey and Brown (1973) and Thorstensson et al (1976a) in control subjects of similar age and anthropometric measurements. The values of peak torque at 180 deg/s were similar to those obtained by Nilsson et al (1977), Thorstensson et al (1977), Thorstensson and Karlsson (1976) and Thorstensson et al (1976a). Nilsson et al (1977) have also reported values for average power and work of left knee extension at 180 deg/s; their values are similar to those of the present investigation.

Fahey and Brown (1973) measured peak torque of elbow extension at 30 deg/s and 180 deg/s in a group of control subjects. Their results are in general agreement with those of the present investigation. Values for average torque (average power) and impulse (work) of elbow extension have not been reported in the literature.

Results of the measurement of ankle plantar flexion strength on the Cybex have not been reported in the literature.

For ankle plantar flexion, knee extension and elbow extension, the extent to which voluntary strength of the right side exceeded that of the left side (6-7%) was in agreement with the findings of Tornvall (1963) for isometric strength measurements. In the present investigation, the extent to which the limb girth of the right side exceeded that of the left side was minimal (calf girth, 0.3%; thigh girth, 0.7%; arm girth, 0%; see also Table 16). Thus, a difference in muscle mass between the two sides was probably not a major factor in the difference in strength between the two sides. The major factor may have been greater neural control of the muscles on the right side. Related to this was the finding that the strength of the right side exceeded that of the left side to a greater extent when measured at a high velocity (8.7%) than when measured at a low velocity (4.5%). There is other evidence that performance dependent upon neural control is better on the right side (for example, see Radford and Upton, 1975).

For left knee extension at 180 deg/s, Nilsson et al (1977) reported a positive correlation between peak torque and work (r = 0.8) and between peak torque and average power (r = 0.87) in 12 control subjects. In the present investigation, the respective correlations were r = 0.59 and r = 0.74 in 25 control subjects. While the correlations were lower in the present investigation, the pattern of a greater correlation between peak torque and work than between peak torque and average power was similar in the two investigations. There have been no other reports in the literature of correlations among the mechanical properties of maximal concentric contractions.

In the present investigation, low correlations in strength were found among different parts of the body (ankle plantar flexion, knee extension and elbow extension); however, in each movement, there was a high correlation between values for the left and right sides. These findings are in agreement with those of Asmussen (1969) and Tornvall (1963); however, relatively high correlations among body parts in isometric strength have been reported by Clarke (1966).

In the control subjects of the present investigation, there was no correlation between voluntary strength and height; this finding is in agreement with that of Tornvall (1963), who found no correlation between isometric strength and height in military conscripts. In the present investigation (V, 3%) and in the study of Tornvall (1963; V, 3.5%), the variation in height was small, and this would account for the low correlation between height and strength. In contrast, the correlation between height and strength in children of different ages is high (Asmussen, 1969). In the present investigation, there was a low positive correlation between body mass and voluntary strength. Tornvall (1963) also found a low positive correlation between body mass and strength. The explanation for the correlation is that a greater body mass is usually associated with greater muscle mass. In addition, the variation in body mass in present investigation (V, 10%) and in the study of Tornvall (1963; V, 11%) was large relative to height (see above). The correlations between limb girth and voluntary strength were moderate to low. The correlations between elbow extension strength and upper arm girth were similar to those reported between arm girth and elbow flexion strength (Carpenter, 1938; Clarke, 1954; Rasch & Morehouse, 1957). A correlation between limb girth and voluntary strength would be expected if it were assumed that limb girth reflected, in part, muscle mass (variation in limb girth also reflects variation in bone size and amount of fat).

The positive correlation between low and high velocity strength found in the present investigation is in agreement with the findings of Lambert (1965) who found a positive correlation between isometric strength and concentric strength measured at different velocities. Thus, it is possible to roughly predict high velocity strength performance from measurements of strength at low velocity. The error in prediction may, however, be large (see discussion of leg strength in athletes below). There is also evidence that as the difference between the velocities at which strength is measured increases, the correlation between low and high velocity strength becomes lower (Bergmaier and Neukomm, 1973; Henry, 1960; Henry and Whitley, 1960; MacIntosh, 1968; Rasch, 1954; Smith, 1969; Whitley and Smith, 1963).

The strength-velocity relation for peak torque in knee extension and elbow extension found in the present investigation (i.e. greater peak torque at 30 deg/s than at 180 deg/s) is similar to that found by Fahey & Brown (1973) for knee extension and elbow extension and by Thorstensson et al (1976a, 1977) for knee extension. Other investigators have observed a smaller peak force produced by high, in comparison to low, velocity concentric contractions (Asmussen et al, 1965; Hill, 1922; Kaneko, 1970; Komi, 1973; Lambert, 1965; Moffroid & Whipple, 1970; Rodgers & Berger, 1974; Wilkie, 1950).

There is an apparent difference between the force-velocity relationship obtained in isolated muscle (e.g. Close, 1972; Hill, 1970, p. 32) and that obtained during voluntary concentric contractions in man. It has been demonstrated and pointed out by Perrine & Edgerton (1978), and also indicated by the data of Komi (1973) and Rodgers & Berger (1974) that the discrepancy occurs at the low end of the velocity range; namely the peak force (in-vivo) at the lowest velocities (including isometric) of contraction was much less than would be expected if the in-vivo force-velocity relationship was the same as that for isolated animal muscle. Perrine & Edgerton (1978) have hypothesized that some neural regulatory mechanism may prevent the attainment of the potentially high levels of force at low velocities of contraction.

Average torque, work and impulse were also less when measured at the higher velocity. Impulse was affected to the greatest extent because it is equal to the product of average torque and duration of contraction, both of which were reduced at the higher velocity.

In contrast, peak and average power were greater at the higher velocity (30 deg/s vs 180 deg/s for knee extension & elbow extension and 6 deg/s vs 36 deg/s for ankle plantar flexion). Similarly, Perrine & Edgerton (1978) found that in knee extension, power increased with increasing velocity up to a joint angular velocity of approximately 240 deg/s. Power decreased slightly at 288 deg/s. According to the data of Thorstensson et al (1976a), knee joint angular velocities of 30 deg/s and 180 deg/s would correspond to 4% and 26% respectively of the maximal knee extension velocity. In knee extension, peak power occurs at 240 deg/s (Perrine & Edgerton, 1978), or at approximately 35% of maximal knee extension velocity. The velocity at which the greatest power is produced has been reported to be between 25-44% of maximal contraction velocity (Astrand & Rodahl, 1977, p. 104; DeVries, 1974, p. 422; Kaneko, 1970). Thus, the most likely explanation for the results of the present investigation is that all velocities selected for testing were on the ascending portion of the power-velocity curve.

The strength-velocity relation ratios for average torque (power) and impulse (work) were significantly greater in elbow extension than in knee extension. The greater ratios for elbow extension may be related to the higher percentage of fast twitch (FT) fibres in the elbow extensor muscles (e.g. long head of triceps, 70% FT, MacDougall et al, 1977) than in the knee extensor muscles (e.g., vastus lateralis, 43-53% FT, Edstrom and Ekblom, 1972; Edstrom and Nystrom, 1969; Gollnick et al, 1974c; Hulten et al, 1975; Jansson and Kaijser, 1977; Komi et al, 1977). In the present investigation, six of the subjects who participated in the training and immobilization experiments and three weight lifters submitted to biopsies of the long head of triceps. The mean percentage of FT fibres was 71% (Elder, G., MacDougall, J. D. and Sale, D. G., unpublished results) and the strength-velocity relation ratios were 0.89, 0.74 and 0.14 for peak torque, average torque and impulse, respectively. Four of the cross country skiers investigated submitted to biopsies of vastus lateralis. The mean percentage of FT fibres was 29% (Elder, G. and MacDougall, J.D., unpublished results) and the strength-velocity relation ratios were 0.74, 0.69 and 0.12 for peak torque, average torque and impulse, respectively. When the data for both muscles were combined, there was a positive correlation between a high percentage of FT fibres and the strength-velocity relation ratio for impulse ($r = 0.55$, $p < 0.05$, $n = 13$). Thorstensson et al (1976a) have also shown a positive correlation between a high percentage of FT fibres in vastus lateralis and a strength-velocity relation ratio (peak torque at 180 deg/s divided by peak torque at 0 deg/s) for knee extension. Further, a positive correlation has been demonstrated between a high percentage of FT fibres in vastus lateralis and high values of peak torque, work and average power of knee extension at 180 deg/s (Nilsson, et al, 1977). In the present investigation, positive correlations were found between the strength-velocity relation ratios and high values for the mechanical properties measured at high velocity, while negative correlations were found between the strength-velocity relation ratios and high values for the mechanical properties measured at low velocity. These results would be predicted on the basis of the findings discussed above.

2. Motor Unit Counts. The mean values for motor unit counts in extensor digitorum brevis, median innervated thenar muscles, hypothenar muscles and soleus are in general agreement with those reported by other investigators using the same method (McComas, 1977; McComas et al, 1971; Sica et al, 1974). One significant difference ($p < 0.005$) was the greater value ($\bar{X} \pm SD$) for the hypothenar muscles (504 ± 128) in comparison to the value reported by McComas (1977, 390 ± 94). The large difference may be explained partly by the small sample (N=14) in the present investigation, for Sica et al (1974) reported a value of approximately 425 ± 75 in a small group of subjects of the same age as those subjects in the present investigation. This value was not significantly different from the value found in the present investigation.

Since the electrophysiological method for counting motor units was first reported (McComas et al, 1971), it has been subjected to some criticisms. Many of the criticisms were anticipated in the initial paper (McComas et al, 1971) and were discussed again when the technique was applied to additional muscles (Sica et al, 1974). Recently, a complete review of the criticisms (with rebuttals) has been published (McComas, 1977, pp. 307-311).

An attempt was made to apply the motor unit counting technique to brachioradialis, because this muscle would have been suitable for training and immobilization experiments. A previous attempt at applying the technique to brachioradialis had not proven successful (McComas et al, 1971). One difficulty cited was the presence in brachioradialis of more than one end plate zone (McComas, 1977, p. 51). An additional difficulty encountered in the present investigation was in obtaining a maximum muscle response (M wave). On many occasions, it was necessary to go to the limits of stimulus strength (400 volts) and duration (500 microseconds) in order to be certain that a maximum M wave had been evoked, and in some cases, the limits were reached without being certain. Related to this difficulty was the larger method error in the measurement of M wave amplitude in brachioradialis in comparison to other muscles.

Despite these difficulties, it was possible to make motor unit counts in many subjects with a reproducibility comparable to that for the other muscles; however, the validity of the results is questionable. One way to assess the validity of the electrophysiological estimates is to compare them with anatomical determinations (McComas, 1977, p. 52). Thus, Feinstein et al (1955) determined motor unit counts for brachioradialis in a male aged 40 years. Values for the left and right sides were 350 and 315 motor units respectively. These values are near the lower limit of the range of values found in the present investigation and were approximately 1.0 SD below the mean value. In EDB (McComas et al, 1971) and in thenar and hypothenar muscles (Sica et al, 1974) there is good agreement between electrophysiological and anatomical determinations. (See also McComas, 1977, p. 52.)

In view of the difficulties with brachioradialis, it was decided to use the thenar muscles for the combined training and immobilization experiments; however, brachioradialis was used in a few training experiments.

The standard deviations of the mean values for motor units within the various muscles were relatively large (approximate average coefficient of variation, 46%). The approximate average coefficients of variation for the other measurements were for M wave amplitude, 30%; reflex potentiation, 56%; isometric twitch tension, 25%; voluntary strength, 23%; motor nerve conduction velocity, 7% and for anthropometry, 5%. The relatively large variability for the motor unit counts and reflex potentiation reflects both the relatively large method errors for these measurements and actual biological variation.

The mean values for maximum M wave amplitude were similar to those reported by other investigators using the same methods for extensor digitorum brevis (Campbell et al, 1973; McComas et al, 1974; Sica and McComas, 1978), thenar muscles (McComas, unpublished results; McComas et al, 1974), hypothenar muscles (McComas et al, 1974) and soleus (Sica and McComas, 1978).

Other factors being equal, one would expect a correlation between the size of the muscle and the amplitude of the maximum M wave. In fact, the M wave amplitude of brachioradialis and soleus, relative to the other muscles (extensor digitorum brevis, thenar and hypothenar) was not as great as expected. There are three factors which could account for this finding. First, the thickness of the skin overlying soleus and brachioradialis is greater in comparison to the other muscles (McComas, A.J., personal communication), and a thicker skin would reduce the amplitude of the recorded M wave. Second, the size of the recorded M wave is related to the closeness of the recording electrode to the end plate zone of the muscle (McComas et al, 1971; Sica et al, 1974). In soleus and brachioradialis, in comparison to the other muscles, it was not possible to place the recording electrode as close to the end plate zone. A third factor, which affected soleus only, was the use of a larger recording electrode; the larger the electrode, the smaller the recorded M wave.

Similarly, one would expect a correlation between mean motor unit potential amplitude and the actual size (number of fibres per unit and diameter of muscle fibres) of the motor units. Feinstein et al (1955) reported mean muscle fibres areas of 25.6, 34.0 and 54.1 microns^2 in the first dorsal interosseus, brachioradialis and medial gastrocnemius, respectively.

The mean number of muscle fibres per motor unit were approximately 340, 410 and 1800, respectively. If it is assumed that soleus is similar to gastrocnemius and that the thenar and hypothenar muscles and extensor digitorum brevis are similar to the first dorsal interosseus, then it would be predicted, on the basis of the anatomical evidence, that the mean motor unit potential amplitude would be greater in soleus and brachioradialis than in extensor digitorum brevis and the small muscles of the hand. In fact, the mean motor unit potential amplitude in brachioradialis was considerably smaller, and in soleus slightly smaller than in these latter muscles. The factors responsible for the discrepancy between the electrophysiological and anatomical findings are the same as those described above for M wave amplitude.

3. Motor Nerve Conduction Velocity. The values for nerve conducti velocity were similar to those reported in the literature (Lawrence and Locke, 1961; Low et al, 1962; McComas et al, 1974; Melvin et al, 1966; Norris et al, 1953; Thomas and Lambert, 1960; Thomas et al, 1959; Trojaborg, 1964; see also LeQuesne, 1971 and Sunderland, 1968).

A positive correlation was found between median and ulnar nerve conduction velocity and between median and deep peroneal nerve conduction velocity. These findings, which to the author's knowledge have not been reported previously, suggest a degree of generality in motor nerve conduction velocity; that is, those who have fast conduction in one nerve are likely to have fast conduction in other nerves. As might be expected, an even higher positive correlation was found between values in the same nerve on the left and right sides. A similar high correlation between left and right ulnar nerve conduction velocity was found by LaFratta and Smith (1964). Lower but significant correlations between left and right ulnar and median nerve conduction velocity were found by Cress et al (1963). These authors also found, in contrast to the findings of the present investigation, that the mean values for the right side exceeded slightly (by 3-4%) those for the left side.

4. <u>Reflex Potentiation</u>. The V_1 potentiation ratios for extensor digitorum brevis and the hypothenar muscles are similar to those reported by Upton and Radford (1975). The V_1 potentiation ratio for the thenar muscles (27.6 ± 13.4) is significantly greater ($p < 0.001$) than the value (15.4 ± 10.0) reported by Upton and Radford (1975) but is not significantly greater than the value (20.5 ± 18, approximate value calculated from data presented in Figure 2) reported by Upton <u>et al</u>, (1971). The larger mean value in the subjects of the present investigation in the thenar muscles and to a lesser extent in extensor digitorum brevis and the hypothenar muscles may be related to the large number of physical education students who were part of the control group. The greater activity level in these subjects and/or a more favourable endowment for motor control may have been responsible for their greater potentiation ratios.

The demonstration of the V_1 wave in brachioradialis is a new finding of the present investigation. The demonstration of a V_1 wave in soleus, using a method similar to that of the present investigation (i.e., supramaximal nerve stimulation and voluntary contraction), has been reported (Gottlieb and Agarwal, 1976). Normal values for the V_1 potentiation ratio in this muscle have not been reported in the literature.

V_2 potentiation ratios in extensor digitorum brevis, thenar and hypothenar muscles have been reported for the first time in the present investigation; however, Upton <u>et al</u> (1971) had previously shown that V_2 waves could be evoked in these muscles during voluntary contraction. In brachioradialis, the V_2 wave had not been previously demonstrated.

In the present investigation, there was no significant difference between values for the right and left sides, nor was there any correlation with "handedness". These findings are in agreement with those of Upton et al (1971).

The symmetry ratios obtained in the present investigation were somewhat lower than those reported by Sica et al (1971). For example, these authors obtained a symmetry ratio of 0.87 ± 0.10 for extensor digitorum brevis in six subjects. The corresponding value in the present investigation was 0.65 ± 0.21. The reason for the difference in the results of the two investigations is not known.

Generally, there was little correlation among muscles in reflex potentiation, although in each muscle there was a positive correlation between values for the left and right sides. These relationships, which have not been previously reported, suggest a specificity in reflex potentiation. A similar specificity was found in voluntary strength and muscle twitch properties.

It has been postulated that the V_1 response consists almost entirely of an H reflex potentiated by voluntary contraction and evidence in support of this hypothesis has been presented (Upton et al (1971). An F wave (Magladery and McDougall, 1950) may be a small part of the V_1 response. There is evidence that the F wave is caused by a recurrent discharge in a few motoneurons resulting from antidromic impulses initiated by nerve stimulation (Dawson and Merton, 1956; Gassel and Wiesendanger, 1965; Mayer and Feldman, 1967; McLeod and Wray, 1966; Thorne, 1965). As postulated (Sica et al 1971; Upton et al, 1971), voluntary contraction potentiates the H reflex by two mechanisms: (1) volition imposes a background facilitation on the motoneurons, which allows the excitatory input from Ia fibres (evoked by nerve stimulation) to raise the motoneurons to threshold, thus initiating the reflex response; (2) "volitional" impulses propagating in motor fibres will collide with antidromic impulses initiated by nerve stimulation, clearing the way for impulses caused by reflex excitation. Were these collisions not to occur, the antidromic impulse might collide with the reflex impulses, preventing the reflex response. Another effect of the antidromic impulse would be, by invading the soma, to render the motoneuron refractory to reflex excitation by the Ia afferents (Gottlieb and Agarwal, 1976).

It has been postulated that the V_2 response consists of a potentiated transcortical reflex (Lee and Tatton, 1975; Milner-Brown *et al*, 1975). The proposed pathway for the reflex (latency, 47-65 ms, Milner-Brown *et al* (1975) is from mechanoreceptors to cuneate nucleus (via a fast conducting pathway such as the dorsal column and medial lemniscus) to ventrobasal thalamus to post-central cortex (areas 1, 2 and 3) to precentral cortex (area 4) to motoneurons (Lee and Tatton, 1975), and these authors present their own evidence and review the evidence of others in support of their hypothesis. More recent evidence for this hypothesis has been presented by Adam *et al* (1976) and Marsden *et al* (1976). The mechanism by which the V_2 response is potentiated during voluntary contraction is to provide background facilitation of motoneurons, upon which the reflex input may be superimposed.

Milner-Brown *et al* (1975) also described a V_3 wave (latency, 74-90 ms). This response was not commonly observed in control subjects, in comparison to the V_1 and V_2 waves. The V_3 response was occasionally observed in the present investigation (e.g. Figure 10C), but was not systematically investigated. It has been postulated that the V_3 response, like the V_2 response, consists of a potentiated transcortical reflex (Lee and Tatton, 1975; Milner-Brown et al, 1975).

The reflex potentiation ratios in the thenar muscles were greater than in the hypothenar muscles and EDB. A similar finding was made by Upton et al (1971), who suggested that the greater potentiation in the thenar muscles may be related to the large cortical area devoted to the control of thumb. In the present investigation, the mean V_1 ratio for soleus was similar to that for the hypothenar muscles, while the potentiation ratios for brachioradialis were similar to those for the thenar muscles. In the case of brachioradialis, it is doubtful that the reason for the relatively large potentiation ratios is the same as in the case of the thenar muscles. Rather, brachioradialis may be relatively more "trained" because of its use as an elbow flexor in the lifting associated with normal activities.

In each muscle (with the exception of soleus, see below) the V_1 and V_2 ratios were similar, and there was a positive correlation between the magnitude of the V_1 and V_2 ratios. These results suggest that the V_1 and V_2 responses are potentiated by the same neural mechanisms (discussed above).

A notable finding was the rare occurrence only of a V_2 wave in soleus. It occurred in a few subjects who produced particularly large V_1 ratios in this muscle, suggesting that the same mechanism responsible for a large V_1 ratio was also responsible for the appearance of the V_2 response. The question arises as to why the V_2 wave occurred only rarely in soleus when the V_1 potentiation ratio in this muscle was comparable to that for EDB and the hypothenar muscles. One possible explanation for the rare occurrence of the V_2 wave in soleus is lesser ability to provide background facilitation of the motoneurons; this possibility is supported by the observation that it is difficult to obtain a full interference pattern in this muscle during maximal voluntary contraction (McComas, A. J., personal communication). If this explanation is correct, it remains to explain the comparatively large V_1 potentiation ratio in soleus, for background facilitation of motoneurons would also be important in the potentiation of the V_1 wave. It will be recalled that voluntary contraction potentiates the V_1 response by providing background facilitation of motoneurons and by "running interference" for the reflex response. The first of these mechanisms is not as important in soleus as in the other muscles, for the H reflex can be elicited at rest in response to stimulation submaximal for motor fibres (Upton et al, 1971) and persists even during flaccid paralysis (Weaver et al, 1963). In contrast, there is strong central depression of the small hand muscles (Oku, 1973), and the H reflex is elicited at rest only when the central depression is not fully developed, as in infants (Thomas and Lambert, 1960) or has been removed (e.g. certain upper motoneuron lesions, Teasdall et al, 1952). The appearance of the H reflex at rest in soleus indicates that Ia afferent input to the motoneurons is powerful enough by itself to cause a reflex response. It is known that the density of Ia synaptic terminals on slow twitch motor units is greater than on fast twitch motor units in the cat (Burke, 1968a, b) and the soleus in man contains a high percentage of slow twitch motor units (Edgerton et al, 1975b; Edstrom and Nystrom, 1969; Johnson et al, 1973; Gollnick et al, 1974c). It has also been shown that it is the slowest motor units within soleus that contribute to the H reflex (Buchtal and Schmalbruch, 1970, 1976; McIlwain and Hayes, 1977; Messina and Cotruto, 1976). Further, the small motoneurons of soleus have a large Ia receptiveness and their EPSP's are larger (Eccles et al, 1957). Therefore, the primary role of voluntary contraction in the potentiation of the H reflex (i.e. V_1 wave) after supra maximal stimulation of the nerve is to run interference for the reflex response, whereas the potentiation of the V_2 response requires a sufficient background facilitation upon which input from the long loop reflex can be superimposed. Thus, a level of voluntary effort which runs adequate interference for potentiation of the V_1 wave may not facilitate adequately those motoneurons participating in the V_2 response.

5. Muscle Twitch Properties. The results of the measurement of isometric twitch properties in extensor hallucis brevis were similar to those reported previously using the same method (Campbell et al, 1973; McComas et al, 1973; Sica and McComas, 1971).

Muscle twitch properties of the median innervated thenar muscles have not been reported previously; however, several studies have been made of the ulnar innervated adductor pollicis (Desmedt et al, 1968; Marsden and Meadows, 1970; Slomic et al, 1968; Takamori et al, 1971). In these investigations, the values obtained for contraction and half relaxation time were similar to those obtained in the present investigation for the median innervated thenar muscles.

The values obtained for contraction time and half relaxation of the hypothenar muscles were in general agreement with those obtained by Burke et al (1974a) for abductor digiti minimi.

The results for triceps surae were similar to those previously reported for contraction time (Buller et al, 1959; Lambert et al, 1951; Marsden and Meadows, 1970; McComas and Thomas, 1968) and half relaxation time (Marsden and Meadows, 1970; McComas and Thomas, 1968) using different techniques.

In the present investigation, several of the triceps surae twitch recordings showed a "notch" on the rising phase (see Figure 13). This feature was also observed by Burke et al (1974b) and Marsden and Meadows (1970). It has been suggested that the initial rapid rise in tension is caused by contraction of gastrocnemius and is succeeded at the "notch" by the slow rise in tension caused by contraction of soleus (Burke et al, 1974b). In different subjects, the prominence of the "notch" varied and was absent in some cases. This variation may be related to the variation in fibre type distribution that is known to occur in these two muscles (Costill et al, 1976; Edgerton et al, 1975b; Gollnick et al, 1974c).

There was little or no correlation found between twitch tension and contraction time. Only in triceps surae was there a positive, significant but low correlation. On the basis of the findings in the weight lifters (stronger and slower triceps surae twitches relative to controls), a higher correlation between twitch tension and contraction time might have been expected; however, another factor which would contribute to variation in contraction time is fibre type distribution which, within a given muscle, shows interindividual variation (for example, see Gollnick et al, 1974c).

In the hypothenar muscles and triceps surae, there was a higher postive correlation between twitch tension and rate of tension development than between twitch tension and contraction time. The correlation between peak tension and rate of tension development has also been observed in voluntary isometric contractions (Stothart, 1973; Willems, 1973).

There is a positive correlation between muscle mass or cross sectional area of muscle and muscle strength (Ikai and Fukunaga, 1968). Two estimates of muscle mass are limb girth and maximum M wave amplitude. The latter has been used to reflect the muscle atrophy that occurs with aging (Campbell et al, 1973) and in neuromuscular disease (for example, see Sica and McComas, 1978). The author had the opportunity to investigate a young man who had contracted poliomyelitis as a child. The disease had affected one leg only. The twitch tension of triceps surae on the affected and normal sides was 2.7 and 100.0 N respectively. The corresponding values were for calf girth, 20.3 and 33.0 cm; soleus M wave amplitude, 4.6 and 12.5 mV; soleus motor units, 200 and 1001 and for reflex potentiation, 17 and 24%. These data also illustrate how limb girth and M wave amplitude can reflect variation in muscle mass and demonstrate the correlation between muscle size and strength. In the group of control subjects investigated, however, there was no correlation between M wave amplitude and twitch tension in any of the muscles investigated. In triceps surae, there was only a low correlation between calf girth and twitch tension, and no correlation between calf girth and soleus M wave amplitude. Thus, it is evident that while the interrelationships among muscle mass, M wave amplitude and muscle strength are revealed when extremes are compared, the correlations are not readily apparent in a relatively homogenous control group. Also relevant in this regard was the low correlation between calf girth and voluntary strength of ankle plantar flexion in a similar control group.

In subjects in whom the twitch properties of more than one muscle were measured, there were no correlations among the muscles in any of the twitch properties. In triceps surae, twitch properties were measured on both right and left sides in some subjects; there was a positive correlation in all twitch properties between values for the left and right sides. These findings were similar to those found for voluntary strength and indicate a specificity in muscle strength.

The results of the triceps surae twitch measurements in male and female control subjects are of interest, for they show that while the females possessed a slightly weaker twitch tension and a smaller calf girth than the males, the contraction time was significantly longer in the females. It is tempting to speculate that the slower twitches in the females is related to a higher percentage of slow twitch fibres in the calf muscles. There are no data available on fibre type distribution of soleus in females; however, no difference has been found between males and females in fibre type distribution of lateral head of gastrocnemius (Costill et al, 1976) and vastus lateralis (Lavoie et al, 1977). Therefore, the current data on fibre type distribution in the muscles of males and females does not support the speculation that the females in the present investigation possessed a relatively high percentage of slow twitch fibres in their calf muscles. However, sex-related differences in fibre composition of skeletal muscle have been found in animals. In the rectus femoris of the rat, the ratio of fast twitch glycolytic to fast twitch oxidative fibres is about 1:1 in the female and 2:1 in the male. The percentage of slow twitch oxidative fibres in the male and female is 1% and 4% respectively. The difference in fibre composition is associated with a longer isometric contraction time in the female rat (Exner *et al*, 1973b). Skeletal muscles have been shown to be sensitive to male sex hormone in the rat (Bass *et al*, 1969) and guinea pig (Bass *et al*, 1971). For example, an increase in the contraction time of the extensor digitorum longus of the rat has been observed following castration (Gutmann, 1970). Therefore, the possibility remains that the longer contraction time in the human females of the present investigation may reflect a real sex-related difference in the calf muscles. It has already been pointed out that the available data on human gastrocnemius indicate no difference between males and females in the percentage of slow twitch oxidative fibres (Costill *et al*, 1976). To the author's knowledge, there are no published data on the ratio of fast twitch glycolytic to fast twitch oxidative fibres in the gastrocnemius of human males and females. Such data might serve to explain the sex-related difference in contraction time found in the present investigation.

C. Training and Immobilization Experiments

1. Voluntary Strength

(a) Effect of training. The subjects who trained elbow extension on the Cybex and with weights increased their peak torque by an average of 73% after an average of 19 weeks of training. It

is difficult to relate this finding to those of other isokinetic strength training studies because of variation in muscle groups trained, and variation in volume, frequency and duration of training. In particular, the duration of training in the present investigation was considerably longer than the longest training periods in comparable studies (8 weeks, Pipes & Wilmore, 1975; Thistle et al, 1967). Taking these factors into consideration the percentage increase in peak torque found in the present investigation was at the upper limit of the range of strength increases with isokinetic training (Komi & Buskirk, 1972; Mannheimer, 1969; Moffroid & Whipple, 1970; Pipes & Wilmore, 1975; Thistle et al, 1967).

In this same group of subjects, average torque and impulse increased by 29% and 25% respectively. There have been no previous reports of changes in average torque (average power) and impulse (work) with isokinetic training.

The group which trained with weights only did not increase strength significantly, as measured on the Cybex. The same results were obtained by Fahey & Brown (1973) and Pipes & Wilmore (1975). Thistle et al (1967) did obtain a significant increase in strength (29%) measured on the Cybex after weight training, but a group which trained on the Cybex made a much larger increase (47%). All of these studies indicate a specificity of training; that is, the closer the method of measurement is to the actual training, the greater the measured improvement. The subjects in the present investigation also had their upper arm girth measured before and after training (MacDougall et al, 1977b). The group which trained both on the Cybex and with weights increased upper arm girth by 7% ($p < 0.005$), while the group which trained only with the weights increased upper arm girth by 10% ($p < 0.005$). The difference between the groups in the increase in arm girth was not significant. Similarly, observation of the subjects' training log books indicated that both groups made similar increases in weight lifting strength. These findings suggest that the specificity of training in the present study (greater Cybex-measured strength in the Cybex-trained group) was a specific adaptation of the nervous system to performing maximal, isokinetic, concentric contractions on the Cybex as a regular part of training.

The correlations among the mechanical properties in the increases with training ($r = 0.59$-0.83) are of interest, for they indicate a considerable independence of adaptation in the mechanical properties. Thus, with a knowledge of the effect of training on one mechanical property, the effect on other mechanical properties can only be roughly predicted. These findings suggest, that it is important to measure all three mechanical properties (peak torque, average torque, impulse) when evaluating the effects of training on muscle strength.

When training progress was monitored frequently, considerable day to day variation in strength was found, although the overall result was a progressive increase in strength. A similar pattern was found by Hettinger and Muller (1953) in the course of isometric strength training. The factors responsible for the day to day variation in strength were probably the same factors responsible for day to day variation in strength in untrained individuals (see discussion of reproducibility of measurements, p.265).

Muller (1962, 1970), Berger (1960) and Gray (1966) observed that the most common training response was a decrease in the rate of progress in the course of training; however, in some experiments, the rate of progress remained constant throughout, and in others, the rate of progress increased in the course of training. In the present investigation, the training response for peak torque was one of gradually decreasing rate of progress, while the responses for average torque and impulse were variable in rate of progress.

There was a large variation in the individual response to elbow extension training; for example, a mean increase in peak torque of 50% after training in a group of six subjects was not statistically significant because the standard error of the mean increase was so large. Two factors contributed to the large variation. One factor was methodological: the results of subjects who trained with weights alone were combined with the results of subjects who trained both on the Cybex and with weights (see above). The second factor was biological variation in the training response. When the same training programme is administered to a group of subjects, the individual variation in response has been observed to be large (Berger, 1960; Brown & Wilmore, 1974; Craikes, 1957; Gray, 1966; Mathews & Kruse, 1957; Jones, 1966; Rose et al, 1957). For example, Jones (1966) found a range in the training increase from -8% to 129% in a group of subjects after isometric training. Rose et al, (1957) reported a range in the increase with isometric training from 80-400%.

Peak torque of isometric thumb abduction increased by an average of 40% after an average of 20 weeks of training. This response to isometric training is within the range of response that has been reported in the literature (Darcus & Salter, 1955; Grimby et al, 1973a, b; Hettinger & Muller, 1953; Muller, 1962, 1970; for a review, see Clarke, 1973).

The increase in elbow extension strength after training can be accounted for in part by adaptive changes within the trained muscles. The subjects who trained elbow extension submitted to needle biopsies of the long head of the triceps muscle before and after training. The reported changes after training included an increase in muscle fibre area (MacDougall et al, 1977a) and an increase in the size and number of myofibrils (MacDougall et al, 1976). A significant increase in limb girth was also observed (MacDougall et al, 1977b). The increased size and number of myofibrils (and thus an increase in the number of myofilaments) would contribute to the increased force of muscle contraction after training. Adaptive changes may also have occurred within the nervous system after elbow extension training, as suggested by the comparison of training results in subjects who trained or did not train on the Cybex (see above). The role of the nervous system in the adaptation to strength training is discussed fully in the INTRODUCTION and is also discussed below in relation to the effects of training on reflex potentiation.

It is difficult to account for the increase in voluntary strength of thumb abduction on the basis of the results of the measurements of changes in the muscle or nervous system. A substantial muscle fibre hypertrophy of the thenar muscles would have been reflected by an increase in the amplitude of the maximum M wave; there was no increase in the amplitude of the maximum M wave. A significant increase in reflex potentiation of the thenar muscles would have indicated adaptive changes within the nervous system; there was no significant increase in the reflex potentiation of the thenar muscles. An increase in voluntary strength in man after training without a significant increase in gross muscle size (Liberson & Asa, 1959; Penman, 1970; Rose et al, 1957; Tanner, 1952; Thorstensson et al, 1976b) or muscle fibre size (Penman, 1970; Thorstensson et al, 1976b) has been previously reported. The findings of Liberson & Asa (1959) are particularly relevant because their study also involved training of the small muscles of the hand (abductors of the fifth finger). Despite a large and significant increase in voluntary strength, these authors found no increase in gross muscle size as measured by three methods (circumference, muscle thickness and soft tissue (X-ray). Thus, the findings of Liberson & Asa (1959) in respect to voluntary strength and gross muscle size were in agreement with those of the present investigation.

It cannot be assumed, however, that lack of increase in gross muscle size after strength training always indicates that no adaptive changes related to increased strength have occurred within the muscle. In training experiments using animals, Goldspink (1964) and Gordon et al (1967b) have demonstrated muscle fibre hypertrophy despite no increase in gross muscle size; Goldspink (1964) postulated that the failure to gain total muscle mass was due to loss of extra cellular tissue. The findings of Liberson and Asa (1959) are of interest in this regard, for these authors found a significant increase in the isometric twitch tension of the trained muscles, although there was no increase in gross muscle size. The increase in isometric twitch tension suggests that muscle fibre hypertrophy may have occurred. In the present investigation, the isometric twitch tension of the thenar muscles decreased after training, in association with an increase in voluntary strength and no change in reflex potentiation and maximum M wave amplitude; however, the decrease in isometric twitch tension may have been related to the method of measurement (see below). Therefore, the increase in voluntary strength of thumb abduction cannot be accounted for by the measurements made on the thenar muscles. It is possible that adaptive changes occurred in other muscles which perform abduction of the thumb (abductor pollicis longus, extensor pollicis brevis) or that adaptive changes occurred within the muscle fibres of the thenar muscles that the measures (maximum M wave amplitude and isometric twitch tension) failed to reflect.

<u>(b) Effect of immobilization</u>. In subjects who immobilized prior to training, an average of approximately five weeks of immobilization resulted in a decrease in elbow extension strength of 26% in peak torque, 26% in average torque and 36% in impulse. The corresponding decrease in thumb abduction strength was 57%. These results are comparable to those of other investigators who have observed the effect of immobilization (in casts) on voluntary strength in man (Dietrick <u>et al</u>, 1948; Hills & Byrd, 1973; Muller, 1970; Stillwell <u>et al</u>, 1967). When training preceded immobilization, the decrease in voluntary strength (in relation to the control values) was smaller after immobilization. Thus, elbow extension strength decreased by 8% in peak torque, 13% in average torque and 22% in impulse. The corresponding decrease in thumb abduction strength was 22%. This finding is of interest, for it could find application in preparation

for joint surgery and subsequent immobilization. For example, in cases where knee extension and flexion strength training could be performed before knee joint surgery, the duration of the post-operative recovery period would be reduced. Also related to this application were the results in three subjects who trained prior to immobilization and in whom voluntary strength was also measured after seven days of recovery from immobilization. After training, elbow extension and thumb abduction strength had increased to 188% and 150% respectively of the control values. After immobilization, elbow extension and thumb abduction strength had decreased to 109% and 79% respectively of the control values. After seven days of recovery from immobilization, elbow extension and thumb abduction strength had incrased to 116% and 100% respectively of the control values. There is evidence that the time required to recover normal (control) strength is greater when immobilization is not preceded by training. Hills & Bird (1973) observed the recovery of hand grip strength in one subject after thirty days of immobilization. Strength decreased by 44% after immobilization and approximately six weeks were required to recover normal strength. Dietrick et al (1948) observed the recovery of plantar flexion strength in four subjects after 6-8 weeks of immobilization. Strength decreased by 21% after immobilization and four weeks were required to recover normal strength.

The results of the investigation of subject CC are of interest, for they show the effect of injury (fractured humerus) superimposed upon immobilization. The duration of immobilization in this subject (6 weeks) was 1.3 SD (28%) greater than the mean duration of immobilization for the other subjects; however, this subject's post immobilization elbow extension strength was approximately 2.8 SD (82%) below the mean value of those subjects who immobilized prior to training. The effect of injury may have been to reduce (by inhibition associated with discomfort) the amount of contractile activity in the muscles of the immobilized limb that is normally evoked by activity of the unrestricted contralateral limb (see below).

The decrease in elbow extension strength after immobilization can be accounted for in part by adaptive changes within the muscles. The subjects underwent needle biopsies of the long head of triceps after immobilization; a decrease in muscle fibre area was found (MacDougall et al, 1977a). A decrease in limb girth was also observed (MacDougall et al, 1977b). Other investigations in man have demonstrated a decrease in limb girth (Dietrick et al, 1948; Ingemann-Hansen & Halkjaer-Kristensen, 1977; Patel et al, 1969), limb volume (Ingemann-Hansen & Halkjaer-Kristensen, 1977; Sargeant & Davies, 1977) and muscle fibre size (Edstrom, 1970; Patel et al, 1969; Sargeant et al, 1977) after immobilization. Further, the "sparing effect" of prior training on the decrease in voluntary strength after immobilization could be accounted for in part by a similar effect upon the decrease in muscle fibre area after immobilization (MacDougall et al, 1977a).

Subject CC had been immobilized because of a fractured humerus. The very low level of voluntary strength following immobilization (noted above) was associated with a greater degree of muscle fibre atrophy in comparison to that of the other subjects who immobilized (MacDougall, J. D., unpublished results).

From the data obtained in the present investigation, it cannot be determined whether adaptive changes within the nervous system contributed to the decrease in voluntary strength of elbow extension.

The decrease in thumb abduction strength after immobilization could be accounted for in part by adaptive changes within the nervous system; the decrease in voluntary strength was associated with a significant decrease in reflex potentiation of the thenar muscles (discussed more fully below). There was no change in the size of the thenar muscles, as measured by maximum M wave amplitude. Furthermore, there was no significant change in isometric twitch tension of the thenar muscles after immobilization; however, this result may have been related to the method of measurement (see below). Therefore, the data obtained in the present investigation did not reflect any changes which may have occurred in the thenar muscles after immobilization; in contrast, the marked decrease in reflex potentiation suggests that neural adaptation contributed substantially to the observed decrease in voluntary strength.

2. Motor Unit Counts

(a) Effect of training. The decision to observe the effect of training upon the number of motor units within muscles was prompted by the finding of low values in some athletes (McComas, A. J., unpublished observations; see also the motor unit counts of gymnasts in RESULTS). The question arose as to whether the reduced motor unit counts were an effect of training per se or the result of repeated trauma associated with participation in the sport. The results of the present investigation indicate that short-term (10-20 weeks) strength traing does not change the number of motor units within muscles. The possibility that long-term strength training or repeated trauma may account for the reduced motor unit counts in some athletes will be discussed further below in relation to the observations made on weight trainers and gymnasts.

(b) Effect of immobilization. Immobilization had no effect upon motor unit counts or M wave amplitude. Therefore, the loss of voluntary strength could not be accounted for by a decrease in the number of functioning motor units or a decrease in motor unit size within the median innervated thenar muscles.

3. Motor Nerve Conduction Velocity

(a) Effect of training. Overall, there was no effect of strength training upon motor nerve conduction velocity. This result is in agreement with findings of a similar investigation (Burke, 1971). However, strength training has been associated with a decrease in monosynaptic reflex time (Francis & Tipton, 1969; Reid, 1967; Tipton & Karpovich, 1966), and it has been postulated that the decrease in reflex time is caused by an increase in nerve conduction velocity associated with nerve fibre hypertrophy (Reid, 1967). If this postulation is accepted, it can be concluded that the effect of strength training upon motor nerve conduction velocity is not uniformly consistent. Variation in intensity and duration of training and variation in muscle groups trained are factors which could account for the inconsistent results. It is interesting to note that when small muscles such as the thenar and hypothenar muscles and extensor digitorum brevis have been trained (present investigation; Burke, 1971), training has had no effect upon nerve conduction velocity. In contrast, when larger muscle groups (quadriceps femoris, triceps surae) are trained (Francis & Tipton, 1969; Reid, 1967; Tipton & Karpovich, 1966), training has apparently caused an increase in motor nerve conduction velocity. The effect of strength training upon nerve conduction velocity is discussed further in the INTRODUCTION and below in relation to the results of motor nerve conduction velocity measurements in weight trainers and gymnasts.

(b) Effect of immobilization. In relation to the control values, immobilization of the thenar muscles had no effect upon median motor nerve conduction velocity. In the group which trained prior to immobilization, however, nerve conduction velocity after training was slightly (3%) though significantly ($p < 0.05$) greater than after immobilization. To the author's knowledge, no similar studies in man have been reported, and the results of animal experiements have not been uniform (see INTRODUCTION). Therefore, further studies on the effect of immobilization upon nerve conduction velocity are required before conclusions can be drawn.

4. Reflex Potentiation

(a) Effect of training. In a series of related experiments, the V_1 and V_2 potentiation ratios increased by 25% and 21% respectively after training. One previous investigation by Milner-Brown et al (1975) had failed to show significant changes in reflex potentiation after six weeks of strength training in four subjects. Thus the present investigation, involving more subjects and longer periods of training, has demonstrated for the first time a significant increase in reflex potentiation after strength training.

The neural pathways and mechanisms underlying the V_1 and V_2 waves have been discussed above in relation to the results of the control experiments. Milner-Brown et al (1975) have postulated that these pathways are strengthened as a result of training and account for the greater reflex potentiation and motor unit synchronization observed in weight lifters. There was a positive correlation ($r = 0.54$) between the increase in V_1 and V_2 potentiation with training, which suggests a common underlying adaptive mechanism.

The question arises as to how the enhanced neural pathways could increase the force of maximal voluntary contractions. The findings of Ikai and Steinhaus (1961) are relevant to this question, for they suggest that under normal conditions many (but not all, Merton, 1954) untrained individuals are unable to recruit all available motor units and to fire all motor units at the maximum possible firing rates, and that with training, increased motor unit recruitment and firing rates of motor units are possible. Thus, it is suggested that the adaptive change within the nervous system, reflected by reflex potentiation, that increases voluntary strength is increased recruitment and firing rates of motor units brought about by strengthened descending neural pathways to motoneurons.

The results of the present investigation have demonstrated that the measurement of reflex potentiation provides a quantitative method for assessing neural adaptation to strength training. This method, and that of Milner-Brown _et al_ (1975) for quantitating motor unit synchronization, make measurable what in the past (see INTRODUCTION) has largely been only speculated upon; namely, adaptive changes within the nervous system after strength training in man.

A further discussion of the effects of strength training upon the nervous system is contained in the INTRODUCTION.

(b) Effect of immobilization. The overall effect (in relation to control values) of approximately five weeks of immobilization was a significant decrease in reflex potentiation of the median innervated thenar muscles (V_1, 39%; V_2, 31%). No comparable studies of the effects of immobilization on the human nervous system have been reported. The decrease in reflex potentiation suggests that the decrease in voluntary strength after immobilization may be accounted for in part by adaptive changes within the nervous system. Extending the discussion above in relation to training, the decrease in reflex potentiation may reflect a weakening of descending neural pathways excitatory to motoneurons, resulting in an inability to recruit all available motor units.

If discomfort were associated with voluntary contraction after immobilization, inhibition might be responsible for the observed decrease in reflex potentiation. However, none of the subjects reported discomfort under these conditions; rather, the reported perception was an inability to contract the thenar muscles strongly.

The pattern of recovery of reflex potentiation following release from immobilization was observed in a few subjects only. After one week of recovery, reflex potentiation had increased to approximately 80% of the control value and after three weeks of recovery to 85% of the control value. The pattern of recovery was similar to that reported for voluntary strength (Dietrick et al, 1948; Hills & Byrd, 1973).

5. Muscle Twitch Properties

(a) Effect of Immobilization

(1) Tension. Approximately five weeks of immobilization resulted in a nonsignificant increase (6%) in twitch tension of the median innervated thenar muscles. No other studies of the effect of immobilization upon the twitch properties of human muscle have been reported; however, in a study designed to simulate the type of immobilization encountered in many clinical situations, Edgerton et al (1975a) observed the effects of six months of immobilization of the hind limb of the Lesser Bushbaby. The findings included a nonsignificant increase (18%) in the twitch tension of the plantaris muscle and a 10% decrease (NS) in tetanic tension. Thus the findings of the present investigation are similar to those reported by Edgerton et al (1975a) with respect to twitch tension. Other investigations

have demonstrated a significant decrease in twitch tension after immobilization in guinea pig gastrocnemius (Maier et al, 1976), cat soleus, gastrocnemius and flexor digitorum longus (Cooper, 1972) and in the soleus and tibialis anterior of the kitten (Mann & Salafsky, 1970) but no significant change in guinea pig soleus (Maier et al, 1976).

The findings of Edgerton et al (1975a) are of particular interest because the nonsignificant changes in absolute twitch and tetanic tension of the plantaris muscle after immobilization were associated with significant decreases in muscle fibre diameter and muscle weight. The question arises as to how a muscle which loses weight and undergoes fibre atrophy is able to maintain its absolute twitch and tetanic tension; further, when expressed per gram of muscle (specific tension), twitch and tetanic tension actually increased significantly. Maier et al (1976) have discussed possible mechanisms which would serve to answer the above question. The mechanism most related to the present investigation was the effect of an immobilization-induced decrease in compliance (extensibility) of the muscle on the recorded tension. For a fixed length, a less compliant muscle would be expected to transfer actively developed tension more effectively from sarcomeres to connective tissue (Maier et al, 1976). A loss of muscle extensibility following immobilization has been reported (Alder et al, 1959; Goldspink et al, 1974; Tabary et al, 1972; Woo et al, 1975).

In the present investigation, the nonsignificant increase in twitch tension of the thenar muscles after immobilization was associated with a significant decrease in voluntary strength and reflex potentiation and no change in maximum M wave amplitude. One interpretation of these combined results is that no atrophy (implied by no change in M-wave amplitude) or loss of contractile strength occurred within the muscles and that the decrease in voluntary strength was accounted for entirely by adaptive changes in the nervous system (as reflected by the decrease in reflex potentiation). An alternate interpretation is that muscle fibre atrophy did occur but was not reflected by the measurement of maximum M wave amplitude or, as in the investigation by Edgerton _et al_ (1975a) cited above, by isometric twitch tension. If this latter interpretation is correct, then it is possible that the decrease in muscle extensibility after immobilization may have "masked" the effect of muscle fibre atrophy upon contractile strength of the thenar muscles.

The measurement of twitch tension of the thenar muscles involved placing an initial tension of 1.0 kg (= 9.8N) upon the muscles. Sica and McComas (1971) have shown that the proportion of the maximum possible twitch tension that is evoked with an initial tension of 1.0 kg is greater in older than in young subjects, and these authors suggested that this age-related effect was caused by reduced elasticity in the muscles of older subjects. There is evidence that elasticity and extensibility of human muscle decrease with age (Bick, 1961; Chapman, 1971; LaBella & Paul, 1965; Wright & Johns, 1960a, b). It is possible that immobilization-induced loss of extensibility would have a similar effect upon the relationship between initial tension and the proportion of maximum possible tension evoked. Thus, after immobilization, an initial tension of 1.0 kg would evoke a higher proportion of the maximum possible tension and mask the effect of immobilization upon contractile strength.

With the present data, it is not possible to determine which of the two interpretations discussed above is correct.

<u>(2) Contraction time</u>. There was a nonsignificant increase (4%) in contraction time after immobilization. Following immobilization, nonsignificant increases in contraction time have also been found in the plantaris muscle of the Lesser Bushbaby (Edgerton <u>et al</u>, 1975a) and in guinea pig gastrocnemius (Maier <u>et al</u>, 1976). A significant increase in contraction time has been observed in the gastrocnemius and flexor digitorum longus of the cat (Cooper, 1972).

In the investigation of Edgerton <u>et al</u> (1975a), the nonsignificant change in contraction time of the predominantly fast twitch plantaris muscle was associated with nonsignificant changes in fibre type distribution. This finding suggests that no change in fibre type distribution may have occurred in the immobilized thenar muscles which, according to the data of Johnson <u>et al</u> (1973), would contain approximately 60% type I (slow twitch oxidative) fibres.

In contrast, the predominantly slow twitch soleus of the guinea pig (Maier <u>et al</u>, 1976), cat (Mann & Salafsky, 1970) and rat (Booth & Kelso, 1973a; Fischback & Robbins, 1969) respon[illegible] to immobilization with a significant decrease in contraction time. In the guinea pig soleus, the decrease in contraction time was associated with a conversion of some slow twitch (low ATPase-activity) fibres to fast twitch (high ATPase-activity) fibres, and in the soleus muscle of the Lesser Bushbaby, immobilization results in a decrease in the percentage of slow twitch oxidative fibres and an increase in the percentage of fast twitch oxidative glycolytic fibres (Edgerton et al, 1975a).

(3) Half relaxation time. Immobilization resulted in a significant 18% increase in half relaxation time. Nonsignificant increases in half relaxation time of the plantaris muscle of the Lesser Bushbaby (7%, Edgerton et al, 1975a) and guinea pig gastrocnemius (12%, Maier et al, 1976) have been reported following immobilization, while Cooper (1972) observed a significant increase in half relaxation time of cat gastrocnemius and flexor digitorum longus muscles.

(4) Rate of tension development. There was no change (2% decrease, NS) in rate of twitch tension development. Nonsignificant decreases in rate of tetanic tension development following immobilization have been reported for the plantaris of the Lesser Bushbaby (Edgerton et al, 1975a) and guinea pig gastrocnemius (Maier et al, 1976).

(b) Effects of training

(1) Tension. Training of the triceps surae resulted in a nonsignificant decrease (2%) in twitch tension. Edgerton (1976) observed a nonsignificant decrease (15%) in the twitch tension of the gastrocnemius of the Lesser Bushbaby after weight lifting training; a significant 22% increase in tetanic tension was obtained. Changes within the muscle included a 20% increase in muscle wieght and an

increase in the concentration of total and myofibrillar protein. Apparently, the measurement of tetanic tension is a better indicator than twitch tension of the changes in contractile strength in muscle following strength training. The measurement of tetanic tension was not performed in the present investigation because of the extreme discomfort it would have caused to the subjects.

However, Liberson & Asa (1959) reported a significant increase in twitch tension of the abductor digiti minimi muscle in man after isometric strength training, and Gonyea & Bonde-Petersen (1978) found significant increases in both twitch and tetanic tension of the palmaris longus and flexor carpi radialis muscles of the cat after weight lifting training. The changes in contractile properties in the latter investigation were associated with an increase in gross muscle size and muscle fibre hypertrophy (Gonyea & Ericson, 1976) and an increase in muscle fibre number (Gonyea et al, 1977). The different results obtained in the various investigations may be related to variation in the intensity and duration of training, as suggested by Gonyea & Bonde-Petersen (1978).

The results for the thenar and hypothenar muscles and extensor digitorum brevis were combined because of a common procedure in the measurement of twitch properties; namely, subjecting the muscle to an initial tension of 1.0 kg (9.8N). The effect of strength training in these muscles was a significant 21% decrease in twitch tension. It has already been pointed out above that twitch tension may not be a sensitive monitor of training-induced adaptation within the muscle; however, the finding of a significant decrease in twitch tension after training requires comment.

In the discussion of the effects of immobilization upon twitch tension, it was hypothesized that an immobilization-induced loss of muscle extensibility would affect the measurement of twitch tension; that is, an initial tension of 1.0 kg would evoke a higher proportion (in relation to the control value) of the maximum possible twitch tension and mask the effect of immobilization upon contractile strength. In contrast, there is evidence that muscle training (including isometric training) causes an increase in muscle extensibility (Booth & Gould, 1975; Chapman, 1971; Less et al, 1977). Therefore, it is possible that a training-induced increase in muscle extensibility had an effect opposite to that of immobilization on the measurement of twitch tension; namely, an initial tension of 1.0 kg would evoke a smaller (relative to control) proportion of the maximum possible twitch tension. If the effect were large enough, it would not only mask any effect of training upon contractile strength, but could conceivably account for the significant decrease in twitch tension obtained after training.

(2) Contraction time. In the combined results for thenar and hypothenar muscles and EHB and for triceps surae, there was no significant change in contraction time after training. However, in one group of subjects, there was a significant decrease in contraction time of the thenar muscles after training. Weight lifting training had no effect upon the contraction time of gastrocnemius of the Lesser Bushbaby (Edgerton, 1976). Isometric training had no effect upon the contraction time of soleus and rectus femoris of the male rat (Exner et al, 1973b). However, a significant increase in contraction time has been observed in the palmaris longus and flexor carpi radialis of the cat (Gonyea & Bonde-Petersen, 1978) and the soleus of the female rat (Exner et al, 1973a) while a significant decrease in contraction time after

training has been observed in the rectus femoris of the female rat (Exner et al, 1973a). In the investigation by Gonyea & Bonde-Petersen (1978), it was shown that the increase in contraction time could not be accounted for by a change in fibre type distribution within the muscles, despite an increase in muscle fibre number.

(3) Half relaxation time. Training resulted in a significant increase (7%) in half relaxation time of the triceps surae muscle; this result was associated with a nonsignificant 4% increase in contraction time. To the author's knowledge, this is the first report of slowing of human muscle by strength training. A significant increase in half relaxation time and contraction time has been observed in the weight trained muscles of cats (Gonyea & Petersen, 1978) while Edgerton (1976) observed a nonsignificant increase (11%) in the half relaxation time in the gastrocnemius of the Lesser Bushbaby. Gonyea & Bond-Petersen (1978) have shown that the increase in half relaxation time was not related to a change in fibre type distribution.

In the combined results for the thenar and hypothenar muscles and extensor digitorum brevis, training had no effect upon half relaxation time.

(4) Rate of tension development. Training resulted in a significant 18% decrease in the rate of twitch tension development when the results for the thenar and hypothenar muscles and extensor digitorum brevis were combined. In triceps surae, the corresponding significant decrease was 9%. Gonyea and Bonde-Petersen (1978) found a significant decrease in the rate of tetanic tension development in the weight trained muscles of cats while Edgerton (1976) reported no significant change in the rate of tetanic tension development in the weight trained gastrocnemius of the Lesser Bushbaby.

In the thenar and hypothenar muscles and extensor digitorum brevis, the decrease in rate of tension development was associated with a significant decrease in twitch tension, no significant change in contraction time and no change in muscle size, as measured by maximum M wave amplitude. In contrast, the decrease in rate of tension development in the investigation of Gonyea & Bonde-Petersen (1978) was associated with significant increases in twitch tension and contraction time and in muscle size. Therefore, the decrease in rate of tension development in the two studies may be related to different mechanisms.

6. Response of the Immobilized Thenar Muscles to Activity of Other Muscle Groups

It was observed that voluntary contraction of the finger flexors and elbow flexors of the non-immobilized limb evoked motor unit activity in the immobilized thenar muscles; furthermore, there was a positive correlation between this effect and the force and duration of contraction of the contralateral muscles. A similar phenomenon has been demonstrated in "resting" non-immobilized muscles of a limb during voluntary contractions of the contralateral limb (Gregg et al, 1957; Sills & Olson, 1958; Stish, 1958). Even greater motor unit activity in the immobilized thenar muscles occurred when the fingers of the immobilized limb performed a light task (tying shoe laces). These results suggest that some motor unit activity occurred in the immobilized muscles as the subjects conducted normal daily activities. Immobilization in the Lesser Bushbaby (Edgerton et al, 1975a) and in the rat (Fischbach & Robbins, 1969) was associated with markedly reduced but not abolished motor unit activity in the immobilized muscles. Therefore, immobilization causes a severe reduction in muscle activity in comparison to the normal condition; however, it cannot be assumed that the immobilized muscles were completely inactive ("disused").

D. Anthropometry, Voluntary Strength and Electrophysiological Measurements in Weight Trainers.

1. Anthropometric Measurements. The values for the weight trainers, expressed as a proportion of the values for control subjects (weight trainers/controls) were for height, 0.98; body mass, 1.21; calf girth, 1.05; thigh girth, 1.12; and arm girth, 1.27. Rasch (1975, p. 61) reported anthropometric data obtained on 33 "Mr. America" winners from 1940-1974. Their values, expressed as a proportion of the control values of the present investigation, were for height, 1.00; body mass, 1.28; calf girth, 1.16; thigh girth, 1.18; and arm girth, 1.54. The values for both groups of weight trainers follow a similar pattern, indicating that the weight trainers of the present investigation are representative of the total population of weight trainers.

Similarly, the control subjects are representative of the population of males of the defined age group. This can be shown by expressing the values for the weight trainers of the present investigation as a proportion of the values of a group of control subjects of similar age investigated by Wilmore (1974); they were for height, 0.98; body mass, 1.19; calf girth, 1.07; thigh girth, 1.13; and arm girth, 1.35. These values are almost identical to those given above in relation to the control group of the present investigation.

The values are greater in the "Mr. America" winners than in the weight trainers of the present investigation. This would be expected for two reasons. First, the champion body builders would, by virtue of being champions, possess the greatest muscle mass and limb girths of all weight trainers. Second, some of the weight trainers in the present investigation were competitive weight lifters rather than body builders, and these individuals train specifically for strength rather than increased muscle size. There is a recognized difference between strength training and body building (Homola, 1968, p. 17; Kirkley, 1963, p. 11; Lamb, 1978, p. 151; MacQueen, 1954; Rasch, 1975, p. 2; Richford, 1966, p. 16).

The weight trainers were similar to the controls in height but possessed a significantly greater body mass. The greater body mass would be accounted for by the greater muscle mass, as indicated by the girth measurements.

The weight trainers exceeded the controls to a greater extent in arm girth than in thigh girth and especially in calf girth. There are two possible explanations for these results. First, it may be more difficult to increase the size of the thigh and in particular the calf muscles by weight training than the arm muscles; many weight training authorities have made this observation (Fallon & Saunders, 1960, p. 91; Franz, 1969, p. 16; Kirkley, 1963, p. 36; O'Shea, 1976, p. 58; Rader, 1956, p. 26; Rasch, 1975, p. 44; Richford, 1968, p. 21; Steiner, 1974, p. 67). Further, there is experimental evidence that the legs are more difficult to develop than the arms (Delorme <u>et al</u>, 1952; Fahey & Brown, 1973; Pipes & Wilmore, 1975;

Stromme et al, 1974; Tanner, 1952; Ward, 1963; Wilmore, 1974). Second, because the thighs and in particular the calves are so difficult to develop, weight trainers become discouraged and stop training them as intensely as the arm muscles. This view has been asserted by some weight training authorities (Fallon & Saunders, 1960, p. 91; Richford, 1968, p. 11). In addition, there is more incentive to develop large arm muscles than large calf muscles (O'Shea, 1976, p. 37).

It is interesting to note that when the values for the "Mr. America" winners are compared to those of the weight trainers in the present investigation, the former exceed the latter to a greater extent in calf and arm girth than in thigh girth. In competitive body building, large calf and arm muscles as well as thigh muscles are required for success. On the other hand, in competitive weight lifting (some of the weight trainers in the present investigation were competitive weight lifters), strength of the thigh muscles is most important for success. Little specific training of the calf muscles occurs; these muscles are trained incidentally during the squat or deep knee bend exercise. While competitive weight lifters, especially power lifters who compete in the bench press, train the elbow extensors, the elbow flexors are neglected in training. Tornvall (1963) has shown that while competitive weight lifters exceed controls by approximately 75% in isometric elbow extension strength, the former exceed the latter by only 25% in elbow flexion strength.

2. Voluntary Strength. The strength of the weight trainers

exceeded that of the controls to the greatest extent in elbow extension, to a lesser extent in knee extension and to the least extent in ankle plantar flexion. This same pattern was observed by Tornvall (1963), who measured isometric strength in 15 weight lifters. The interpretation of these findings is the same as the one presented above in relation to the girth measurements. It is worth noting that the pattern of the relationship between the values of the weight trainers and controls (i.e. weight trainers/controls) was the same for limb girth and voluntary strength; namely, elbow extension-arm girth greater than knee extension-thigh girth greater than ankle plantar flexion-calf girth.

When the results of the weight trainers and control subjects were combined, there was no correlation between voluntary strength and height; however, there was a low positive correlation between body mass and strength. This latter correlation was not as great when computed from the control values alone. Adding the data from the weight trainers increased the range of values for the two variables and this served to strengthen the correlation. Other factors being equal, the greater body mass is associated with greater muscle mass which in turn is associated with greater strength.

The difference in strength between weight trainers and controls was reduced when strength was expressed per kg body mass rather than absolutely. This reduction in difference is the result of the greater body mass of the weight trainers relative to controls.

The correlation between limb girth and strength was greater when the results of the weight trainers and controls were combined than when the correlation was computed from the control data alone.

The reason for the greater correlation in the former case has been discussed above in relation to the correlation between strength and body mass.

The correlation between arm girth and elbow extension strength was greater than between thigh girth and knee extension strength or between calf girth and ankle plantar flexion strength. This finding is probably related to the fact that training of the arms is more often associated with increased muscle size than is the case when the legs are trained (see above). Further, leg strength may be increased by training without any increase in muscle size as measured by limb girth (Penman, 1970; Tanner, 1952; Thorstensson et al, 1976b; Ward, 1963; Wilmore, 1974) and muscle fibre size (Penman, 1970; Thorstensson et al, 1976b).

When the results for the weight trainers were combined with those of the control subjects the correlations between low and high velocity strength, among the mechanical properties and among the three movements were greater than when the correlations were computed from the control data alone. The reason for this finding has been discussed above in relation to the strength-body mass relationship and strength-limb girth relationship.

Generally, there was no difference between the weight trainers and control subjects in the strength-velocity relation. Thorstensson et al (1976a) demonstrated a positive correlation between a strength-velocity relation ratio in knee extension and a high percentage of fast twitch fibres in vastus lateralis. Therefore, the lack of difference between the weight trainers and control subjects in the strength-velocity relation for knee extension suggests that these two groups possessed a similar fibre type composition in the knee extensor muscles. This suggestion is supported by the findings of Edstrom & Ekblom (1972), Gollnick et al (1972) and Prince et al (1976) which indicated that weight lifters possess a fibre type composition (percentage of slow twitch fibres in vastus lateralis) similar to that of control subjects. It is possible that the similarity between the two groups in the strength-velocity relation for ankle plantar flexion and elbow extension is also associated with a similarity in the fibre type composition of the involved muscles.

In low velocity strength, the symmetry ratios in the weight trainers were consistently greater than in the controls; however, the difference was not significant. The trend toward greater symmetry in the weight trainers is not surprising when it is considered that the weight lifting exercises employed by these individuals are bilateral and that successful execution of the exercises requires a high degree of similarity in strength between the two limbs.

3. Motor unit counts. There was no difference between the weight trainers and the control subjects in thenar and soleus motor unit counts. These results are in agreement with those of the training experiments, which revealed no change in motor unit counts after short term training. The combined results suggest that strength training per se does not cause a reduction in the number of motor units within muscles.

It should be pointed out, however, that while the thenar muscles are suitable for electrophysiological measurements, they are probably not trained intensely by weight lifters in comparison to other muscles. It is tempting to refer to the lack of significant differences between the weight trainers and controls in reflex potentiation and in isometric twitch tension of the thenar muscles as evidence in support of this assertion. However, in the training experiments, the thenar muscles failed to respond (in terms of reflex potentiation) to intense, specific training over a period of approximately 20 weeks, and the twitch tension decreased significantly. Thus, while it is reasonable to assert that the thenar muscles were not intensely trained by the weight trainers, the negative results in regard to thenar reflex potentiation and twitch tension cannot be used without reservation in support of this assertion. The weight trainers possessed a greater median motor nerve conduction velocity than the controls. This finding supports the contention that the thenar muscles were trained to some degree. Further, the fact that thenar twitch tension was 13% (NS) greater in the weight trainers than in the controls, while the twitch tension was significantly less (20%) after short term training, suggests that strength may have increased in the thenar muscles to the point where it overcame to some extent the effect of increased muscle extensibility upon the measurement of twitch tension (see discussion of effect of training upon twitch tension).

In contrast, there is strong evidence that the triceps surae (of which soleus is a portion) was fairly intensely trained in the weight trainers, although not as intensely as the knee extensors and elbow extensors (see above). Voluntary strength of plantar flexion, isometric twitch tension of triceps surae and reflex potentiation of soleus were all greater in the weight lifters than the controls. Therefore, the motor units results in soleus do constitute evidence that strength training <u>per se</u> does not cause a reduction in the number of motor units within muscles.

4. M wave amplitude. There was no difference between the weight trainers and controls in thenar and soleus maximum M wave amplitude. These results are in agreement with the results of the control and training experiments, which indicated that there was little correlation between maximum M wave amplitude and limb girth or twitch tension except when extreme values were compared.

5. Motor nerve conduction velocity. Median motor nerve conduction velocity was 8% greater in the weight trainers than in the controls. Deep peroneal, but not median nor ulnar, motor nerve conduction velocity was significantly greater in the gymnasts than in the controls. Kato (1960) and Lastovka (1969) found no difference between athletes and controls in ulnar motor nerve conduction velocity; however, Lastovka (1969) did find a significant difference between athletes and controls in posterior tibial motor nerve conduction velocity. Upton and Radford (1975) found no difference between elite sprinters and controls in median ulnar or peroneal motor nerve conduction velocity. Thus, these studies comparing athletes with controls, and the training studies discussed above have not produced uniformly consistent results. In the case of the studies on athletes, variation in calibre of athletes, type of athletes and extent of training could account in part for the variation in results.

6. Reflex potentiation. Reflex potentiation in the soleus was greater in the weight trainers than in the controls. Similarly, the gymnasts were superior to controls in reflex potentiation of brachioradialis and extensor digitorum brevis; however, the differences were not statistically significant. Upton & Radford (1975)

found that elite sprinters were superior to controls in reflex potentiation of the thenar and hypothenar muscles and extensor digitorum brevis. Milner-Brown <u>et al</u> (1975) observed high values of reflex potentiation in the thenar muscles of weight lifters.

The question arises as to the relative contributions that genetic endowment and training make to the superior reflex potentiation observed in athletes. The consistently high values in the elite sprinters in three muscles not specifically related to sprinting suggest that genetic endowment has a decisive role. On the other hand, the results of the training experiments indicate that training may play an important role. The results in the weight trainers also support the role of training. In soleus, a muscle fairly intensely trained by the weight trainers, reflex potentiation was superior, while in the thenar muscles, which are not intensely trained, reflex potentitaion was not superior in the weight trainers. The results of Milner-Brown <u>et al</u> (1975) also indicate the importance of training, for these authors observed that the superior reflex potentiation in weight lifters decreased during lapses in training. Thus, the available data suggest that both endowment and training account for the high values of reflex potentiation observed in athletes. The relative contributions of these two factors probably vary depending upon the sport and its related training.

<u>7. Muscle twitch properties</u>. Twitch tension and contraction time of triceps surae in the weight trainers were significantly greater than in the controls; half relaxation time was also greater in the weight trainers, but the difference was not statistically significant. In the thenar muscles, a similar trend was observed, but the differences

were not significant. Related to these findings are the data of Upton & Radford (1975) which showed that the twitch contraction time and half relaxation time in extensor hallucis brevis were significantly longer in elite sprinters than controls. Strength training resulted in a "slowing" of the triceps surae twitch (see above); thus, the similar results in the athletes may be related to the activity or training involved in the sports.

A functional advantage of a longer twitch contraction and half relaxation time is that a greater impulse (twitch tension x time) would be delivered per action potential.

In the weight trainers, the results of the measurement of rate of twitch tension development are of interest, for while the contraction time was 20% greater in the weight trainers than controls, the rate of twitch tension development was only 2% (NS) less; the greater (16%) twitch tension in the weight trainers apparently compensated for the longer contraction time. It should also be noted that the strength-velocity relation ratios of the weight trainers were similar to those of the controls (see above).

The "slow" twitch contraction of the sprinters (Upton & Radford, 1975) seems inappropriate in view of the nature of sprinting. More appropriate to the nature of sprinting is the reported high percentage of fast twitch fibres in the vastus lateralis (Gollnick et al, 1972; Komi et al, 1976; Thorstensson et al, 1977) and gastrocnemius (Costill et al, 1976) of sprinters. Sprinters have also been shown to possess superior strength-velocity relation ratios in knee extension (present investigation) and superior high velocity knee extension strength, expressed per kg body mass (Thorstensson et al, 1977). Komi et al (1977) reported superior "power" (power test of Margaria et al, 1966) in sprinters.

The underlying mechanism of the increased contraction time is unknown. Gonyea & Bonde-Petersen (1978) observed that the weight trained muscles of the cat became larger, stronger and slower but there was no change in the percentage of slow twitch fibres. These findings suggest that an increased contraction time is, for some reason, a concomitant of enlarged, stronger muscles. However, in the present investigation, strength training of triceps surae resulted in a slower twitch despite no change in twitch tension (the tetanic tension might have increased, had it been measured, see Edgerton, 1976). In addition, the control experiments revealed little correlation between twitch tension and contraction time.

E. Electrophysiological Measurements in Gymnasts

1. Motor unit counts. The motor unit counts were significantly reduced in the thenar and hypothenar muscles and in extensor digitorum brevis (EDB) of the gymnasts. In soleus and brachioradialis, the motor unit counts were normal. Mean motor unit potential amplitude was significantly greater in the hypothenar muscles, while in the thenar muscles, the greater value in the gymnasts was not significant. In the soleus, brachioradialis and EDB, the difference between gymnasts and controls in this measure was small and non-significant. Maximum M wave amplitude in EDB was significantly reduced in the gymnasts; in the remaining muscles, there was no significant difference.

The reduced motor unit counts in distal rather than more proximal muscles may be the result of more intense use of the former in gymnastics. This interpretation is unlikely because gymnasts use the proximal muscles investigated as much if not more than the distal muscles. Further, the results of the training experiments and the investigation of weight trainers indicated that intense training of proximal or distal muscles does not cause a reduction in the number of motor units. A more likely interpretation for the results is that the reduction in motor units in the distal muscles is the result of repeated trauma to the associated nerve fibres as they pass through the ankle and wrist. Tumbling and vaulting frequently result in soreness and sprains of the ankles and wrists, and it is not uncommon for gymnasts to have their ankles and wrists taped for support (personal observations; the author is a former gymnastic coach and competitor). One female gymnast, who was twelve years old and who possessed a motor unit count in EDB of 130 at the time of investigation, was forced to retire three years later because of chronic ankle sprains. Mechanical stress has also been implicated in the ulnar neuropathy observed in cyclists (Eckman et al, 1975) and in the finding of denervation in EDB in otherwise healthy subjects (Jennekens et al, 1972).

In the hypothenar muscles, the pattern of reduced motor units and increased mean motor unit potential amplitude observed in the gymnasts was similar to that observed in elderly subjects (Sica et al, 1974). These latter findings were interpreted as indicating that surviving motoneurons can reinnervate denervated muscle fibres. Similar findings in EDB have been interpreted in the same way (Campbell et al, 1973). While in the elderly the denervation of muscle fibres is caused by death of motoneurons, in the gymnasts the denervation may be caused by nerve fibre injury. It is of interest that an apparently similar process of adaptation occurs in response to both conditions (aging and nerve injury). An important but as yet unanswered question is to what extent the motoneurons will recover when the gymnasts retire from active participation.

In EDB the reduction in motor units in the gymnasts was associated with a reduction in mean motor unit potential amplitude. The reason for the difference in response between EDB and the hypothenar muscles is unknown. Sica _et al_ (1974) observed a difference between the thenar and hypothenar muscles in the response to aging; namely, the thenar motoneurons were unable to enlarge their muscle fibre population to the same extent as the hypothenar motoneurons. The findings in the EDB of the gymnasts suggest that the motoneurons had a lesser capacity (relative to hypothenar motoneurons) for reinnervating denervated muscle fibres.

2. Nerve conduction velocity. The deep peroneal motor nerve conduction velocity was greater in the gymnasts than controls. There was no difference between the groups in median or ulnar nerve conduction velocity. These findings have been discussed in relation to the findings in the weight trainers (see above).

In three gymnasts, median and ulnar sensory conduction velocity were measured along with the response amplitudes. The values obtained were compared with control values reported by McComas _et al_ (1974). Both median and ulnar conduction velocity were greater than in the controls, but only in the median nerve was the difference significant (10%, $p < 0.01$). In both the median and ulnar nerves, the response amplitudes were significantly reduced in the gymnasts, by 17% ($p < 0.01$) and 42% ($p < 0.001$) respectively. These latter results agree with the observed motor unit counts in suggesting trauma to the nerves.

3. Reflex potentiation. The gymnasts were superior to controls in reflex potentiation of EDB and brachioradialis; however, the differences were not significant. These findings have been discussed in relation to the findings in weight trainers (see above).

4. Muscle twitch properties. Generally, there was no difference between the gymnasts and controls in the twitch properties of triceps surae; however, the contraction time of the female gymnasts was significantly shorter than that of the controls. The half relaxation time and twitch tension were also less in the gymnasts, but the differences were not significant. The reason for the difference between groups in contraction time is unknown. The female gymnasts were 12-13 years of age while the female controls were ($\bar{X} \pm$ SD) 23 ± 7 years of age. The calf girth of the gymnasts was 31.2 ± 3.1 cm while the corresponding value in the controls was 34.6 ± 1.7 cm; the difference between groups was not significant. If the difference between groups is age related, it is of interest that the opposite relationship (i.e. "speeding" of the twitch between childhood and early adulthood) has been observed in males (McComas *et al*, 1973).

F. Knee Extension Strength in Athletes

1. Low velocity strength. The weight lifters possessed greater strength than the controls. This anticipated result has

also been found by Edstrom & Ekblom (1972) and Tornvall (1963). In contrast, the cross country skiers, who were endurance athletes, possessed less strength than controls. The same result was found by Komi et al (1977). The sprinters were equal to (in impulse) or inferior to (in peak and average torque) the controls. In other investigations sprinters have been found to be stronger than control subjects (Ikai, 1964; Komi et al, 1977; Thorstensson et al, 1977). The high level of strength (impulse) in the cyclists suggests that these athletes require both strength and endurance for successful performance. The cyclists of the present investigation possessed a mean maximal oxygen uptake of 67.8 ml/kg/min (MacDougall, J. D., unpublished results). Burke et al (1977) found a maximal oxygen uptake of 67.1 ml/kg/min in competitive cyclists. These values are considerably greater than those reported for control subjects (Astrand & Rodahl, 1977, p. 408) and weight lifters (Edstrom & Ekblom, 1972; Gollnick et al, 1972) but less than that reported for cross country skiers (Astrand & Rodahl, 1977, p. 408). In the present investigation, the maximal oxygen uptake of the cross country skiers was 66.4 ml/kg/min.

In the medial gastrocnemius of the cat, the fast twitch glycolytic and fast twitch oxidative glycolytic fibres have a greater estimated specific tension (tension per unit cross sectional area of muscle) than the slow twitch oxidative fibres (Burke & Edgerton, 1975). If the same situation exists in man, then individuals with larger fast twitch fibres in a given muscle, a higher percentage of fast twitch fibres and a larger fast twitch/slow twitch fibre area ratio would tend to have stronger muscles. Weight lifters and controls have been shown to have a similar fibre type distribution in vastus lateralis (Edstrom & Ekblom, 1972; Gollnick et al, 1972; Prince et al, 1976); however, weight lifters possess larger fast twitch fibres and a greater fast twitch (FT)/slow twitch (ST) fibre area ratio (Edstrom & Ekblom, 1972; Prince et al, 1976). Power athletes (sprinters, jumpers) possess a higher percentage of FT fibres (Gollnick et al, 1972; Komi et al, 1977; Thorstensson et al, 1977) and a greater FT/ST fibre area ratio (Thorstensson et al, 1977) than controls. Cyclists possess a fibre type distribution and a FT/ST fibre area ratio similar to that of controls but possess larger FT and ST fibres in vastus lateralis (Burke et al, 1977) Cross country skiers have a relatively low percentage of FT fibres in vastus lateralis (Komi et al, 1977; MacDougall, J.D. & Elder, G., unpublished results). Thus, the observed variations in strength in the different groups of athletes can be accounted for in part by variation in muscle composition. Other factors affecting strength performance are gross muscle size and neural control (see discussion of the results in weight trainers and controls).

All groups of athletes performed best in relation to controls in impulse and worst in peak torque. This finding may be related to the fact that impulse is a measure of the total effect of the muscle contraction (i.e. the integration of the torque-time recording) while peak torque is only the highest point on the torque-time recording (see Figure 2 in METHODS). Whatever the reason for the finding, it demonstrates the value of measuring impulse and average torque in addition to the commonly measured peak torque. For reasons that are not apparent, the pattern was most marked in the cyclists and sprinters and least marked in the cross country skiers and weight lifters (Figure 38).

With the exception of the weight lifters, the body mass of the controls and the remaining athletic groups was similar; therefore, the strength performance in these latter groups in relation to controls was the same whether strength was expressed absolutely or per kg body mass. In contrast, the weight lifters possessed a significantly greater body mass than controls; consequently, when strength was expressed per kg body mass rather than absolutely, the difference between the weight lifters and controls was reduced. This finding has been discussed above in relation to the investigation of the weight trainers.

A comparison of strength in the weight lifters and cyclists is of interest. In peak torque and average torque expressed absolutely, the weight lifters were superior to the cyclists, while in impulse the cyclists were superior to the weight lifters. The cyclists exceeded the weight lifters in both average torque and impulse when values were expressed per kg body mass. These findings are difficult to interpret; however, they further demonstrate the value of measuring all three properties when evaluating the strength performance of athletes. In addition, they reveal the impressive strength performance of the cyclists, who compare favourably with the weight lifters.

2. High velocity strength. The performance of the weight lifters, cyclists and cross country skiers in relation to controls was similar for both low and high velocity strength. However, the

sprinters performed better at the high velocity than at the low velocity. This characteristic of the sprinters was also revealed in the strength-velocity relation ratios; the sprinters possessed higher values than the other groups. Sprinters possess a high percentage of fast twitch fibres in vastus lateralis (Gollnick et al, 1972; Komi et al, 1977; Thorstensson et al, 1977) and this may account in part for the observed strength performance. A positive correlation between a high percentage of FT fibres in vastus lateralis and high values of a strength-velocity relation ratio in knee extension has been reported by Thorstensson et al (1976a).

The correlations between low and high velocity strength were positive and significant (range: r = 0.66 - r = 0.84). The magnitude of the correlation coefficients permits only a rough prediction of high velocity strength from low velocity strength, as the results in the sprinters demonstrate. In this regard it is interesting to compare the sprinters with the cross country skiers (endurance athletes) in low and high velocity strength. In low velocity strength, the cross country skiers were superior to the sprinters in peak torque and average torque but were inferior in impulse, whereas in high velocity strength the sprinters were superior to the cross country skiers in peak torque, average torque and impulse. These results serve to emphasize the importance of measuring strength at different velocities when evaluating the strength performance of athletes.

At both low and high velocities, the correlations between strength and body mass, among the mechanical properties and between left and right sides were similar to those observed in the control experiments (see above).

V. SUMMARY

The purpose of the present investigation was to observe the effects of strength training and immobilization upon neuromuscular function in man. The measures of neuromuscular function selected for the investigation were voluntary strength and a number of electrophysiological measurements, including motor unit counts, nerve conduction velocity, reflex potentiation, and the contractile properties of isometric twitch contractions.

To fulfill the purpose of the investigation, three kinds of experiments were conducted. First, healthy, untrained subjects participated in training and immobilization experiments. Second, measurements were made in selected groups of athletes. Weight lifters and gymnasts received special attention because these athletes require a high level of voluntary strength for successful performance. The other groups of athletes included cyclists, cross country skiers and sprinters. The experiments on athletes provided cases of long term training. Third, measurements were made on healthy control subjects. The results of these measurements provided a basis for comparison with the athletes; control experiments were also conducted to establish the reproducibility of the measurements.

The results of the investigation are summarized below.

Voluntary Strength

1. Training resulted in an increase in voluntary strength.

This was shown in the short term (10-20 weeks) training experiments. Training of elbow extension resulted in an increase in the peak torque (power), average torque (power) and impulse (work) of maximal concentric muscle contractions. Training of thumb abduction increased the peak torque of maximal isometric contractions. In the weight lifters who provided cases of long term training, voluntary strength of plantar flexion, knee extension and elbow extension was greater than in controls. In cyclists, who must possess both strength and endurance, knee extension strength was enhanced, while in the cross country skiers, who require primarily endurance, knee extension strength was not enhanced. The sprinters exceeded the controls only in high velocity impulse of knee extension.

2. In elbow extension, there was a positive correlation between the increase in peak torque and average torque, between the increase in peak torque and impulse and between the increase in average torque and impulse. However, the correlations were only moderately high, suggesting that there could be considerable independence in the increases of the three mechanical properties. The results in the athletes provided an example of this independence. Thus, all groups of athletes performed better in relation to controls in impulse than in peak or average torque; this pattern was most marked in cyclists and sprinters. These findings served to indicate the importance of measuring all three mechanical properties when assessing the effects of training programmes or evaluating the strength of athletes.

3. The results in control subjects and athletes showed a positive correlation between relatively low and relatively high velocity strength

performance; however, the correlation coefficients were only moderately high, allowing room for many "exceptions to the rule". The sprinters were an exception in the present study. These athletes performed much better at high velocity than would be predicted from their low velocity performance.

4. When measured at high velocity, peak torque, average torque, impulse and work were less, and peak and average power were greater than when measured at low velocity.

5. In average torque (power) and impulse (work), the strength-velocity relation ratio (value at high velocity/value at low velocity) was greater for elbow extension than knee extension.

6. The weight lifters were similar in height to the control subjects, but possessed greater body mass and greater calf, thigh and arm girth. These findings suggest that the greater strength of the weight lifters was due in part to their greater muscle mass. Further support for this suggestion came from the observation that when strength was expressed per kg body mass rather than absolutely, the difference between the weight lifters and the controls was reduced. Another indication of the importance of muscle mass was the correlation between strength and limb girth. The weight lifters exceeded the controls to the greatest extent in elbow extension strength and arm girth and to the least extent in ankle plantar flexion strength and calf girth.

7. In a group of subjects that trained elbow extension both with weight lifting and with concentric contractions on an isokinetic dynamometer, the increase in strength, as measured on the isokinetic

dynamometer, was greater than in a group of subjects that trained by weight lifting only. Both groups made similar increases in weight lifting strength and arm girth. These results suggest a specificity of training; that is, a test of voluntary strength that is dissimilar to the method of training will underestimate the adaptation that has occurred. These results also suggest that the nervous system as well as the muscle is involved in the adaptation to strength training.

8. Voluntary strength of elbow extension (peak torque, average torque, impulse) and thumb abduction (peak torque) decreased following immobilization.

9. In elbow extension, there was a positive correlation between the decrease in peak torque and average torque, between peak torque and impulse and between average torque and impulse.

10. Training prior to immobilization had a "sparing" effect; that is, strength decreased less in relation to control values after immobilization than when training did not precede immobilization.

Motor Unit Counts

1. In relation to the control condition, short term strength training had no effect on motor unit counts or M wave amplitude in the muscles investigated (median innervated thenar, hypothenar, extensor digitorum brevis, brachioradialis, soleus).

2. As cases of long term strength training, the weight lifters exhibited motor unit counts (thenar, soleus) similar to those of control subjects. These findings, together with the results of the short

term training experiments, suggest that training per se does not affect motor unit counts.

3. In the gymnasts, motor unit counts were normal in proximal muscles (brachioradialis, soleus) but were reduced in distal muscles (thenar, hypothenar, extensor digitorum brevis). On the basis of these findings, it was hypothesized that trauma-induced injury to nerves at the wrist and ankle was responsible for the reduced motor unit counts. Trauma to the wrists and ankles is common in gymnastics.

4. In relation to the control condition, immobilization had no effect upon thenar motor unit counts; however, in one group of subjects that immobilized prior to training, the post training value was greater than the post immobilization value.

5. Immobilization had no effect upon M wave amplitude.

Nerve Conduction Velocity

1. In relation to the control condition, short term strength training had no effect upon motor nerve conduction velocity in the nerves investigated (median, ulnar, deep peroneal).

2. As cases of long term strength training, the weight lifters exhibited a median motor nerve conduction velocity greater than that of controls.

3. As cases of long term strength training, the gymnasts possessed greater than normal conduction velocity in deep peroneal motor and median sensory nerves but normal values for median and ulnar

motor and ulnar sensory nerve conduction velocity.

4. In relation to the control condition, immobilization had no effect upon median motor nerve conduction velocity; however, in a group of subjects that immobilized prior to training, the post training value was greater than the post immobilization value.

5. While the results of the experiments were not uniformly consistent, there was some support for the suggestion that nerve conduction velocity may change in response to training and immobilization.

6. In the gymnasts, the median and ulnar sensory nerve response amplitudes were reduced in relation to control values. These results were interpreted (as were the reduced thenar and hypothenar motor unit counts) as indicating trauma-induced injury to the nerves at the wrist.

Reflex Potentiation

1. Short term strength training caused an increase in reflex potentiation.

2. As cases of long term strength training, weight lifters exhibited a greater than normal level of reflex potentiation in soleus but a normal level in the thenar muscles.

3. On the basis of the short term training results and the results in weight lifters, it was concluded that adaptation occurs within the nervous system in response to strength training, as reflected by an increase in reflex potentiation. It was hypothesized that the increase in reflex potentiation was associated with an increased ability

to recruit motor units and to discharge them at high rates. These changes would increase voluntary strength.

4. Immobilization caused a decrease in reflex potentiation. This finding was interpreted as indicating that adaptation occurs within the nervous system in response to immobilization. It was hypothesized that the decrease in reflex potentiation was associated with decreased ability to recruit motor units and to discharge them at high rates. These changes would contribute to the decrease in voluntary strength caused by immobilization.

Muscle Twitch Properties

1. In the combined results for thenar and hypothenar muscles and extensor digitorum brevis, short term strength training caused a decrease in twitch tension; however, it was hypothesized that this result was the effect upon the technique of measurement of an increase in muscle extensibility caused by strength training.

2. In triceps surae, short term strength training had no effect upon twitch tension.

3. As cases of long term training, weight lifters exhibited greater than normal twitch tension in triceps surae but not in the thenar muscles.

4. In the combined results for thenar and hypothenar muscles and extensor digitorum brevis, short term strength training had no effect upon contraction time and half relaxation time; however, in the thenar muscles alone, training resulted in a decrease in contraction

time. It was hypothesized that this finding was also the effect of a training-induced change in muscle extensibility.

5. In triceps surae, short term strength training had no effect upon contraction time but caused an increase in half relaxation time.

6. As cases of long term training, weight lifters exhibited greater than normal contraction time of triceps surae.

7. In the combined results for thenar and hypothenar muscles and extensor digitorum brevis and in triceps surae, short term strength training resulted in a decrease in rate of twitch tension development.

8. Immobilization of the thenar muscles had no effect upon twitch tension, rate of tension development or contraction time but caused an increase in half relaxation time. However, it was hypothesized that these results may have been affected by an immobilization-induced decrease in muscle extensibility.

REFERENCES

Adam, J., C. D. Marsden, P. A. Merton and H. B. Morton (1976) The effect of lesions in the internal capsule and the sensorimotor cortex on servo-action in the human thumb. J. Physiol. 254: 27-28P.

Alder, A. B., G. N. Crawford and R. G. Edwards (1959) The effect of limitation of movement on longitudinal growth. Proc. R. Soc. Biol. B150:554-562.

Andersen, P., and J. Henriksson (1977) Training induced changes in the subgroups of human type II skeletal muscle fibres. Acta physiol. scand. 99:123-125.

Andersson, Y. and J. Edstrom (1957) Motor hyperactivity resulting in diameter decrease of peripheral nerves. Acta physiol. scand. 39:240-245.

Ashworth, B., L. Grimby and E. Kugelberg (1967) Comparison of voluntary and reflex activation of motor units. Functional organization of motorneurones. J. Neurol. Neurosurg. Psychiat. 30:91-98.

Asmussen, E. (1969) The neuromuscular system and exercise. In: Exercise Physiology. Ed. H. B. Falls. New York: Academic Press, pp. 3-42.

Asmussen, E., O. Hansen and O. Lammert (1965) The relation between isometric and dynamic muscle strength in man. Communications from the testing and observations institute of the Danish National Association for Infantile Paralysis, no. 20.

Astrand, P. O. and K. Rodahl (1977) Textbook of Work Physiology. New York: McGraw-Hill.

Barnard, R. J., V. R. Edgerton, T. Furukawa and J. B. Peter (1971) Histochemical, biochemical and contractile properties of red, white and intermediate fibers. Amer. J. Physiol. 220:410-414.

Barnard, R. J., V. R. Edgerton and J. B. Peter (1970) Effect of exercise on skeletal muscle. II Contractile properties. J. Appl. Physiol. 28:767-770.

Barney, V. S. and B. C. Bangerter (1961) Comparison of three programs of progressive resistance exercise. Res. Quart. 32:138-146.

Bass, A., E. Gutmann, V. Hanzlikova, I. Hajek and I Syrovy (1969) The effect of castration and denervation upon the contraction properties and metabolism of levator ani muscle of the rat. Physiol. bohemoslov 18:177-194.

Bass, A., E. Gutmann, V. Hanzlikova and I. Syrovy (1971) Sexual differentiation of enzyme pattern and its conversion by testosterone in the temporal muscle of the guinea pig. Physiol. bohemoslov 20:423-431.

Bates, J. D. (1967) The effects of static and dynamic strength training and position of exercise on the acquisition of strength, speed of movement, reaction time and endurance. Un published D.Ed thesis, Louisiana State University.

Beise, D. and V. Peaseley (1937) The relation of reaction time, speed and agility of big muscle groups to certain sports skills. Res. Quart. 8:133-142.

Berger, R. A. (1960) The effect of varied weight training programs on strength and endurance. Unpublished Ph.D. thesis, University of Illinois.

Bergmaier, G., and P. Neukomm (1973) The correlation between static muscular force and speed of movement. Medicine and Sport, vol. 8: Biomechanics III. Basel: Karger, pp. 235-238.

Bick, E. M. (1961) Aging in the connective tissues of the human musculoskeletal system. Geratrics 16:446-453.

Binkhorst, R. A. (1969) The effect of training on some isometric contraction characteristics of fast muscle. Pfluegers Archiv. 309:193-202.

Binkhorst, R. A. and M. A. van't Hof (1973) Force-velocity relationship and contraction time of the rat fast plantaris muscle due to compensatory hypertrophy. Pfluegers Archiv. 342:145-158.

Booth, F. W., and E. W. Gould (1975) Effects of training and disuse on connective tissue. In: Exercise and Sports Sciences Reviews. Ed. J. F. Keogh. New York and London: Academic Press, 83-112.

Booth, F. W., and J. R. Kelso (1973a) Effect of hindlimb immobilization on contractile and histochemical properties of skeletal muscle. Pfluegers Archiv. 342:231-238.

Booth, F. W. and J. R. Kelso (1973b) Production of rat muscle atrophy by cast fixation. J. Appl. Physiol. 24:404-406.

Bonde-Petersen, F. (1960) Muscle training by static, concentric and eccentric contractions. Acta physiol. scand. 48:406.

Braddom, R. L. and C. Wolfe (1978) Musculocutaneous nerve injury after heavy exercise. Arch. Phys. Med. Rehabil. 59:290-293.

Brown, C. H. and J. H. Wilmore (1974) The effects of maximal resistance training on the strength and body composition of women athletes. Med. Sci. Sports 6:174-178.

Buchthal, F. and H. Schmalbruch (1970) Contraction times and fiber types in intact human muscle. Acta physiol. scand. 79:435-452.

_______ (1976) Contraction times of reflexly activated motor units and excitability cycle of the H-reflex. Prog. Brain Res. 44:367-376.

Buller, A. J., A. C. Dornhorst, R. Edwards, D. Kerr and R. F. Whelan (1959) Fast and slow muscles in mammals. Nature 183:1516-1517.

Burke, D., N. F. Skuse and K. Lethlean (1974a) Isometric contraction of the abductor digiti minimi muscle in man. J. Neurol. Neurosurg. Psychiat. 37:825-834.

_______ (1974b) An analysis of myotonia in para myotonia congenita. J. Neurol. Neurosurg. Psychiat. 37:900-906.

Burke, J. F. (1971) Electrophysiological responses to maximum isometric exercise. Unpublished Ph.D. thesis, Louisiana State University.

Burke, R. E. (1968a) Group Ia synaptic input to fast and slow twitch motor units of cat triceps surae. J. Physiol. 196:605-630.

_______ (1968b) Firing patterns of gastrocnemius motor units in the decerebrate cat. J. Physiol. 196:631-654.

Burke, R. E. and V. R. Edgerton (1975) Motor unit properties and selective involvement in movement. In: Exercise and Sports Sciences Reviews. Ed. J. F. Keogh and J. H. Wilmore. New York: Academic Press, pp. 31-33.

Burke, R. E., K. Kanda and R. F. Mayer (1975) The effect of chronic immobilization on defined types of motor units in cat medial gastrocnemius. 5th Ann. Meeting Soc. Neurosci., New York, p. 763.

Campbell, M. J., A. J. McComas and F. Petito (1973) Physiological changes in ageing muscle. J. Neurol. Neurosurg. Psychiat. 36:174-182.

Carpenter, A. (1938) A critical study of the factors determining effective strength tests for women. Res. Quart. 9:3-29.

Chapman, E. A. (1971) Effects of exercise upon joint mobility of young and old men. Unpublished Ph.D. thesis, University of Southern California.

Chor, H. and R. E. Dokart (1936) A study of simple disue atrophy in the monkey. Amer. J. Physiol. 117:626-639.

Clarke, D. H. (1973) Adaptations in strength and muscular endurance resulting from exercise. In: Exercise and Sport Sciences Reviews. Ed. J. H. Wilmore. New York: Academic Press, pp. 73-102.

Clarke, H. H. (1954) Relationship of strength and anthropometric measures to various arm strength criteria. Res. Quart. 25:134-143.

________ (1966) Muscular Strength and Endurance in Man. Englewood Cliffs, N.J.: Prentice-Hall.

Close, R. I. (1972) Dynamic properties of mammalian skeletal muscle. Physiol. Rev. 52:129-197.

Cohen, H. L. and J. Brumlik (1976) Electroneuromyography: Hagerstown, M.D.: Harper and Rowe.

Cole, W. V. (1960) The effect of immobilization on striated muscle and the myoneural junction. J. Comp. Neurol. 115:9-13.

Coleman, A. E. (1969) Effect of unilateral isometric and isotonic contractions on the strength of the contralateral limb. Res. Quart. 40:490-495.

Considine, W. J. (1966) Reflex and reaction times within and between athletes and non-athletes. Unpublished M.Sc. thesis, Illinois State University.

Cooper, R. R. (1972) Alterations during immobilization and regeneration of skeletal muscle in cats. J. Bone Joint Surg. 54-A:919-953.

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

Costill, D. L., P. D. Gollnick, E. D. Jansson, B. Saltin and E. M. Stein (1973) Glycogen depletion patterns in human muscle fibres during distance running. Acta physiol. scand. 89:374-383.

Craikes, J. G. (1957) An analysis of some aspects of an exercise and training program. Unpublished M.Sc. thesis, University of Oregon.

Cress, R. H., L. S. Taylor, B. G. Allen and R. W. Holden (1963) Normal motor nerve conduction velocities in the upper extremity and their relation to handedness. Arch. Phys. Med. Rehabil. 44:216-219.

Crockett, J. C., V. R. Edgerton, S. R. Max and R. J. Barnard (1976) The neuromuscular junction in response to endurance training. Exp. Neurol. 51:207-215.

Crowder, V. (1966) A comparison of the effects of two methods of strength training on reaction time. Unpublished Master's thesis, Louisiana State University.

Darcus, H. D. (1956) Discussion on an evaluation of the methods of increasing muscle strength. Proc. Roy. Soc. Med. 49:999-1005.

Darcus, H. D. and N. Salter (1955) The effect of repeated muscular exertion on muscle strength. J. Physiol. 129:325-336.

Dawson, G. D. and P. A. Merton (1956) 'Recurrent' discharges from motoneurones. XXth International Physiological Congress, Brussels, 1956. Abstracts of communications, pp. 221-222.

Deitrick, J. E., D. G. Whedon and E. Shorr (1948) Effect of immobilization upon various metabolic and physiologic functions of normal men. Am. J. Med. 4:3-36.

Delorme, T. (1945) Restoration of muscle power by heavy resistance exercises. J. Bone Joint Surg. 27:645-667.

Delorme, T. L., B. G. Ferris and J. R. Gallagher (1952) Effect of progressive resistance exercise on muscle contraction time. Arch. Phys. Med. Rehabil. 33:86-92.

Delorme, T. L., F. E. West and W. J. Shriber (1950) Influence of progressive resistance exercise on knee function following femoral fractures. J. Bone Joint Surg. 32A:910-924.

Desmedt, J. E., B. Emeryk, P. Renoirte and K. Hainaut (1968) Disorder of muscle contraction process in sex-linked (Duchenne) muscular dystrophy, with correlative electromyographic study of myopathic inovlvement in small hand muscles. Am. J. Med. 45:853-872.

de Vries, H. A. (1974) Physiology of Exercise. Dubuque, Iowa: Wm. C. Brown.

Dolley, D. H. (1909) The morphological changes in nerve cells resulting from overwork in relation with experimental anemia and shock. J. Med. Res. 21:95-114.

Durante, G. (1902) Anatomie pathologique des muscles. In: Manuel d'Histologie Pathologique Vol. 2. Ed. V. Cornil and L. Ranvier. Paris: Felix Alcan.

Eccles, J. C. (1944) Investigations on muscle atrophies arising from disuse and tenotomy. J. Physiol. 103:253-266.

_______ (1953) The neurophysiological basis of mind. The Principles of Neurophysiology. Oxford: Claredon.

Eccles, J. C. (1958) Problems of plasticity and organization at simplest levels of mammalian central nervous system. Perspectives Biol. Med. 1:379-396.

Eccles, J. C., R. M. Eccles and W. Kozak (1962) Further investigations on the influence of moto neurones on the speed of muscle contraction. J. Physiol. 163:324-339.

Eccles, J. C., R. M. Eccles and A. Lundberg (1957) The convergence of monosynaptic excitatory afferents on to many different species of alpha motoneurones. J. Physiol. 137:22-50.

Eccles, J. C., K. Krnjevic and R. Miledi (1959) Delayed effects of peripheral severance of afferent nerve fibres on the efficacy of their central synapses. J. Physiol. 145:204-220.

Eccles, J. C. and A. K. McIntyre (1953) The effects of disuse and activity on mammalian spinal reflexes. J. Physiol. 121:492-516.

Eckman, P. B., G. Perlstem and P. H. Altrocchi (1975) Ulnar neuropathy in bicycle riders. Arch. Neurol. 32:130-132.

Edds, M. V. (1949) Experiments on partially deneurotized nerves. Part 2 (Hypertrophy of residual fibres). J. exp. Zool. 112:29-47.

________ (1950) Hypertrophy of nerve fibers to functionally overloaded muscles. J. Comp. Neurol. 93:259-275.

Edgerton, V. R. (1976) Neuromuscular adaptation to power and endurance work. Can. J. Appl. Sport Sci. 1:49-58.

Edgerton, V. R., R. J. Barnard, J. B. Peter, C. A. Gillespie and D. R. Simpson (1972) Overloaded muscles of a non-human primate (Galago senegalenesis). Exp. Neurol. 37:322-339.

Edgerton, V. R., R. J. Barnard, J. B. Peter and A. Meier (1975a) Properties of immobilized hind-limb muscles of Galago senegalenesis. Exp. Neurol. 46:115-131.

Edgerton, V. R., J. L. Smith and D. R. Simpson (1975b) Muscle fiber type populations of human leg muscles. Histochem. J. 7:259-266.

Edstrom, L. (1970) Selective atrophy of red muscle fibers in the quadriceps in long-standing knee joint dysfunction. Injuries to the anterior cruciate ligament. J. Neurol. Sci. 11:551-558.

Edstrom, L. and B. Ekblom (1972) Differences in sizes of red and white muscle fibres in vastus lateralis of musculus quadriceps femoris of normal individuals and athletes. Relation to physical performance. Scand. J. clin. Lab. Invest. 30:175-181.

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

Eisen, A. A., S. Carpenter, G. Karpati and A. Bellavue (1973) The effect of muscle hyper- and hypoactivity upon fibre diameters of intact and regenerating nerves. J. Neurol. Sci. 20:457-469.

Erb, W. (1891) Dystrophia musculorum progressiva. Deutsch. Z. Nervenheilk 1:227-261.

Eriksson, B. O., P. D. Gollnick and B. Saltin (1973) Muscle metabolism and enzyme activities after training in boys 11-13 years old. Acta physiol. scand. 87:485-497.

Exner, G. U., H. W. Staudte and D. Pette (1973a) Isometric training of rats--effects upon fast and slow muscle and modification by an anabolic hormone (Nandrolone Decanoate). I Female rats. Pfluegers Archiv. 345:1-14.

________ (1973b) Isometric training of rats--effects upon fast and slow muscle and modification by an anabolic hormone (Nandrolone Decanoate). II Male rats. Pfluegers Archiv. 345:14-22.

Fahey, T. D. and C. H. Brown (1973) The effects of an anabolic steroid on the strength, body composition and endurance of college males when accompanied by a weight training program. Med. Sci. Sports 5:272-276.

Fallon, M. and J. Saunders (1960) Muscle Building For Beginners. New York: Arc Books.

Feinstein, B., B. Lindegard, E. Nyman and G. Wohlfart (1955) Morphological studies of motor units in normal human muscles. Acta Anat. 23:127-142.

Ferguson, A. B., L. Vaughan and L. Ward (1957) Study of disuse atrophy of skeletal muscle in rabbit. J. Bone Joint Surg. 39:583-596.

Fischbach, G. D. and N. Robbins (1969) Changes in contractile properties of disused soleus muscle. J. Physiol. 201:305-320.

________ (1971) Effect of chronic disuse of rat soleus neuromuscular junctions on postsynaptic membrane. J. Neurophysiol. 34:562-569.

Fischer, E. and V. W. Ramsey (1946) Changes in the protein content and some physicochemical properties of the protein during muscular atrophy of various types. Am. J. Physiol. 145:571-582.

Francis, P. R. and C. M. Tipton (1969) Influence of a weight training program on quadriceps reflex time. Med. Sci. Sports 1:91-94.

Franz, E. (1969) Beginning Weight Training. Belmont, California: Wadsworth.

Friman, G. (1977) Effect of acute infectious disease on isometric muscle strength. Scand. clin. Lab. Invest. 37:303-308.

Gassel, M. M. and M. Wiesendanger (1965) Recurrent and reflex discharges in plantar muscles of the cat. Acta physiol. scand. 65:138-142.

Gerchman, L. B., V. R. Edgerton and R. E. Carrow (1975) Effects of physical training on the histochemistry and morphology of ventral motor neurons. Exp. Neurol. 49:790-801.

Gilliam, T. B., R. R. Roy, J. F. Taylor, W. W. Heusner and W. D. Van Huss (1977) Ventral motor neuron alterations in rat spinal cord after chronic exercise. Experientia 33:665-667.

Goldberg, A. L. (1965) Muscle hypertrophy in hypophysectomized rats. Physiologist 8:175.

________ (1967) Work-induced growth of skeletal muscle in normal and hypophysectomized rats. Am. J. Physiol. 213:1193-1198.

Goldberg, A. L., J. D. Etlinger, D. F. Goldspink and C. Jablecki (1975) Mechanism of work-induced hypertrophy of skeletal muscle. Med. Sci. Sports 7:248-261.

Goldspink, D. F. (1977) The influence of immobilization and stretch on protein turnover of rat skeletal muscle. J. Physiol. 264:267-282.

Goldspink, G. (1964) The combined effects of exercise and reduced food intake on skeletal muscle fibers. J. Cell Comp. Physiol. 63:209-216.

________ (1970) Morphological adaptation due to growth and activity. In: The Physiology and Biochemistry of Muscle as a Food, II. Ed. E. J. Briskey, R. G. Cassens and B. B. Marsh. Madison: University of Wisconsin Press, pp. 521-536; 577-606.

Goldspink, G. and K. F. Howells (1974) Work-induced hypertrophy in exercised normal muscles of different ages and the reversibility of hypertrophy after cessation of exercise. J. Physiol. 239:179-193.

Goldspink, G., C. Tabary, J. C. Tabary, C. Tardieu and G. Tardieu (1974) Effect of denervation on the adaptation of sarcomere number and muscle extensibility to functional length of the muscle. J. Physiol. 236:733-742.

Gollnick, P. D., R. B. Armstrong, B. Saltin, W. Saubert, W. C. Sembrowich and R. E. Shepherd (1973a) Effect of training on enzyme activity and fiber composition of human skeletal muscle. J. Appl. Physiol. 34:107-111.

Gollnick, P. D., R. B. Armstrong, C. W. Saubert IV, K. Piehl and B. Saltin (1972) Enzyme activity and fiber composition in skeletal muscle of untrained and trained men. *J. Appl. Physiol.* 33:312-319.

Gollnick, P. D., R. B. Armstrong, W. C. Sembrowich, R. E. Shepherd and B. Saltin (1973b) Glycogen depletion in human skeletal muscle fibers after heavy exercise. *J. Appl. Physiol.* 34:615-618.

Gollnick, P. D., J. Karlsson, K. Piehl and B. Saltin (1974a) Selective glycogen depletion pattern in skeletal muscle fibres of man following sustained contractions. *J. Physiol.* 241:59-68.

Gollnick, P. D., K. Piehl and B. Saltin (1974b) Selective glycogen depletion pattern in human muscle fibers after exercise of varying intensity and at varying pedalling rates. *J. Physiol.* 241:45-58.

Gollnick, P. D., B. Sjodin, J. Karlsson, E. Jansson and B. Saltin (1974c) Human soleus muscle: A comparison of fiber composition and enzyme activities with other leg muscles. *Pfluegers Archiv.* 348:247-255.

Gonyea, W. and F. Bonde-Petersen (1978) Alterations in muscle contractile properties and fiber composition after weight-lifting exercise in cats. *Exp. Neurol.* 59:75-84.

Gonyea, W. and G. C. Ericson (1976) An experimental model for the study of exercise-induced skeletal muscle hypertrophy. *J. Appl. Physiol.* 40:630-633.

Gonyea, W., G. C. Ericson and F. Bonde-Petersen ~~(1977)~~ Skeletal muscle fiber splitting induced by weight-lifting exercise in cats. *Acta physiol. scand.* 99:105-109.

Goodgold, J. and A. Eberstein (1972) *Electrodiagnosis of Neuromuscular Diseases.* Baltimore: Williams and Wilkins.

Gordon, E. E., K. Kowalski and M. Fritts (1967a) Protein changes in quadriceps muscle of rat with repetitive exercise. *Arch. Phys. Med. Rehabil.* 48:296-303.

________(1967b) Changes in rat muscle fiber with forceful exercises. *Arch. Phys. Med. Rehabil.* 48:577-582.

________(1967c) Adaptations of muscle to various exercises. *J. Amer. Med. Assoc.* 199:139-144.

Gottlieb, G. L. and G. C. Agarwal (1976) Extinction of the Hoffman reflex by antidromic conduction. *Electroencephalogr. Clin. Neurophysiol.* 41:19-24.

Gray, R. K. (1966) An investigation of the individual differences in the response of young adult males to isotonic overload strength exercise. Unpublished Ph.D. thesis, University of Western Australia.

Gregg, R. A., A. F. Mastellone and J. W. Gersten (1957) Cross exercise--A review of the literature and study utilizing electromyographic technique. Amer. J. Phys. Med. 36:269-280.

Grimby, G., P. Bjorntorp, M. Fahlen, T. A. Hoskins, O. Hook, H. Oxhoj and B. Saltin (1973a) Metabolic effects of isometric training. Scand. J. Clin. Lab. Invest. 31:301-305.

Grimby, G., C. Heijne, O. Hook and H. Wedel (1973b) Changes in muscle strength and endurance after training with intermittent maximal isometric contractions. Scand. J. Rehab. Med. 5:118-123.

Grimby, L. and J. Hannerz (1977) Firing rate and recruitment order of toe extensor motor units in different modes of voluntary contraction. J. Physiol. 264:865-879.

Gutmann, E. (1970) Nervous and hormonal mechanisms in the aging process. Exp. Geront. 5:357-366.

Gutmann, E. and I. Hajek (1971) Differential reaction of muscle to excessive use in compensatory hypertrophy and increased phasic activity. Physiol. bohemoslov. 20:205-212.

Gutmann, E., I. Hajek and P. Horsky (1969) Effect of excessive use on contraction and metabolic properties of cross-striated muscle. J. Physiol. 203:46P-47P.

Gutmann, E., I. Hajek and V. Vitek (1970) Compensatory hypertrophy of the latissimus dorsi posterior muscle induced by elimination of the latissimus dorsi anterior muscle of the chicken. Physiol. bohemoslov. 19:483-489.

Gutmann, E., S. Schiaffino and V. Hanzlikova (1971) Mechanism of compensatory hypertrophy in skeletal muscle of the rat. Exp. Neurol. 31:451-464.

Gydikov, A. and D. Kosarov (1974) Some features of different motor units in human biceps brachii. Pfluegers Archiv. 347:75-88.

Haggmark, T., E. Jansson and B. Svane (1978) Cross-sectional area of the thigh muscle in man measured by computed tomography. Scand. J. Clin. Invest. 38:355-360.

Hall-Craggs, E. C. B. (1970) The longitudinal division of fibres in overloaded rat skeletal muscle. J. Anat. 107:459-470.

Hannerz, J. (1974) Discharge properties of motor units in relation to recruitment order in voluntary contraction. Acta physiol. scand. 91:374-384..

Hebb, P. O. (1949) The Organization of Behaviour. New York: Wiley, pp. 255-260.

Helander, E. (1958) Adaptive muscular 'allomorphism'. Nature 182: 1035-1036.

Helander, E. A. S. (1961) Influence of exercise and restricted activity on the protein composition of skeletal muscle. Biochem. J. 78:478-482.

Hellebrandt, F. A. (1951) Cross-education: ipsilateral and contralateral effects of unimanual training. J. Appl. Physiol. 4:136-143.

Hellebrandt, F. A. and S. J. Houtz (1956) Mechanisms of muscle training in man: experimental demonstration of the overload principle. Phys. Ther. Rev. 36:371-383.

Hellebrandt, F. A., A. M. Parrish and S. J. Houtz (1947) Cross-education: the influence of unilateral exercise on the contralateral limb. Arch. Phys. Med. Rehabil. 28:76-85.

Henneman, E. and C. B. Olson (1965) Relations between structure and function in the design of skeletal muscles. J. Neurophysiol. 28:581-598.

Henry, F. M. (1960) Factorial structure of speed and static strength in a lateral arm movement. Res. Quart. 31:440-447.

Henry, F. M. and J. D. Whitley (1960) Relationships between individual differences in strength, speed and mass in an arm movement. Res. Quart. 31:24-33.

Herbison, G. J., M. M. Jaweed and J. F. Ditunno (1978) Muscle fiber atrophy after cast immobilization in the rat. Arch. Phys. Med. Rehabil. 59:301-305.

Hettinger, T. L. and E. A. Muller (1953) Muscular performance and training. Arbeits physiol. 15:111-126.

Hill, A. V. (1922) The maximum work and mechanical efficiency of human muscles, and their most economical speed. J. Physiol. 56:19-41.

_______. (1970) First and Last Experiments in Muscle Mechanics. London: Cambridge University Press.

Hills, W. C. and R. J. Byrd (1973) Effects of immobilization in the human forearm. Arch. Phys. Med. Rehabil. 54:87-90.

Holloszy, J. O. (1975) Adaptation of skeletal muscle to endurance exercise. Med. Sci. Sports 7:155-164.

Holloszy, J. O. and F. W. Booth (1976) Biochemical adaptations to endurance exercise in muscle. Ann. Rev. Physiol. 38:273-291.

Holmes, R. and P. J. Rasch (1958) Effect of exercise on number of myofibrils per fiber in sartorius muscle of the rat. Am. J. Physiol. 195:50-52.

Homola, S. (1968) Muscle training for athletes. West Nyack, New York: Parker.

Honet, J. C., R. H. Jebsen and E. B. Perrin (1968) Variability of nerve conduction velocity determinations in normal persons. Arch. Phys. Med. Rehabil. 49:650-654.

Hulten, B., A. Thorstensson, B. Sjodin and J. Karlsson (1975) Relationship between isometric endurance and fibre types in human leg muscles. Acta physiol. scand. 93:135-138.

Hursh, J. B. (1939) Conduction velocity and diameter of nerve fibers. Am. J. Physiol. 127:131-139.

Hyden, H. (1965) Activation of nuclear RNA of neurons and glia in learning. In: Anatomy of Memory. Ed. D. P. Kimble. Palo Alto, California: Science and Behaviour Books, pp. 178-239.

Ikai, M. (1964) The effects of training on muscular endurance. Proc. Int. Cong. Sport Sci., p. 109.

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

Ikai, M. and A. H. Steinhaus (1961) Some factors modifying the expression of human strength. J. Appl. Physiol. 16:157-163.

Ingemann-Hansen, T. and J. Halkjaer-Kristensen (1977) Lean and fat component of the human thigh. The effects of immobilization in plaster and subsequent physical training. Scand. J. Rehabil. Med. 9:67-72.

Jaffe, D. M., R. D. Terry and A. J. Spiro (1978) Disuse atrophy of skeletal muscle--a morphometric study using image analysis. J. Neurol. Sci. 35:189-200.

Jansson, E., and L. Kaijser (1977) Muscle adaptation to extreme endurance training in man. Acta physiol. scand. 100:315-324.

Jaweed, M. M., E. E. Gordon, G. J. Herbison and K. Kowalski (1974) Endurance and strengthening exercise adaptations. I. Protein changes in skeletal muscle. Arch. Phys. Med. Rehabil. 55:513-516.

Jennekens, F. G. I., B. E. Tomlinson and J. N. Walton (1972) The extensor digitorum brevis: histological and histochemical aspects. J. Neurol. Neurosurg. Psychiat. 35:124-132.

Jewell, P. A. and E. J. Zaimis (1954) Changes at the neuromuscular junction of red and white muscle fibers in the cat induced by disuse atrophy and hypertrophy. J. Physiol. 124:429-442.

Johnson, M. A., J. Polgar, D. Weightman and D. Appleton (1973) Data on the distribution of fiber types in thirty-six human muscles. An autopsy study. J. Neurol. Sci. 18:111-129.

Jones, R. E. (1966) A neurological interpretation of maximum isometric training and its relationship to individual training variability. Unpublished Ph.D. thesis, University of Wisconsin.

Kandell, E. R. and W. A. Spencer (1968) Cellular neurophysiological approaches in the study of learning. Physiol. Rev. 48:65-134.

Kaneko, M. (1970) The relation between force, velocity and mechanical power in human muscle. Res. J. Phys. Educ. (Japan) 14:141-145.

Karlsson, J., B. Diamont and B. Saltin (1971) Muscle metabolites during submaximal exercise in man. Scand. J. Clin. Invest. 26:385-394.

Karlsson, J., L. O. Nordesjo, L. Jordfeldt and B. Saltin (1972) Muscle lactate, ATP and CP levels during exercise after physical training in man. J. Appl. Physiol. 33:199-203.

Karlsson, J., B. Sjodin, A. Thorstensson, B. Hulten and K. Frith (1975) LDH isozymes in skeletal muscles of endurance and strength trained athletes. Acta physiol. scand. 93:150-156.

Karpati, G. and W. K. Engel (1968) Correlative histochemical study of skeletal muscle after suprasegmental denervation, peripheral nerve section and skeletal fixation. Neurol (Minneap) 18:681-692.

Karpovich, P. V., R. R. Dering and M. Ikai (1960) Reflex and reaction time. Report to U.S. Army Medical Research and Development Command, Office of Surgeon General, pp. 1-8.

Kato, M. (1960) The conduction velocity of the ulnar nerve and the spinal reflex time measured by means of the H wave in average adults and athletes. Tohoku J. exp. Med. 73:74-85.

Keller, L. F. (1942) The relation of 'quickness of bodily movement' to success in athletics. Res. Quart. 13:146-155.

Kirkley, G. W. (1963) Weight Lifting and Weight Training. New York: Arc Books.

Knapp, B. N. (1961) Simple reaction times of top-class sportsmen and research students. Res. Quart. 32:409-411.

Komi, P. V. (1973) Relationship between muscle tension, EMG and velocity of contraction under concentric and eccentric work. In: New Developments in Electromyography and Clinical Neurophysiology. Vol. 1. Basel: Karger, p. 596.

Komi, P. V. and E. R. Buskirk (1972) Effect of eccentric and concentric muscle conditioning on tension and electrical activity of human muscle. Ergonomics 15:417-434.

Komi, P. V., H. Rusko, J. Vos and V. Vihko (1977) Anaerobic performance capacity in athletes. Acta physiol. scand. 100:107-114.

Komi, P. V., J. T. Viitasalo, M. Havu, A. Thorstensson and J. Karlsson (1976) Physiological and structural performance capacity: effect of heredity. In: Biomechanics V-A. Ed. P. V. Komi. Baltimore: University Park Press, pp. 118-123.

Konorski, J. (1950) Mechanisms of Learning. In: Physiological Mechanisms in Animal Behaviour. New York: Academic Press.

Kowalski, K., E. E. Gordon, A. Martinez and J. Adamek (1969) Changes in enzyme activities of various muscle fiber types in rat induced by different exercises. J. Histochem. Cytochem. 17:601.

LaBella, F. S. and G. Paul (1965) Structure of collagen from human tendon as influenced by age and sex. J. Geront. 20:54-59.

LaFratta, C. W. and O. H. Smith (1964) A study of the relationship of motor nerve conduction velocity in the adult to age, sex and handedness. Arch. Phys. Med. Rehabil. 45:407-412.

Lamb, D. R. (1978) Physiology of Exercise. New York: Macmillan.

Lambert, E. H., L. O. Underdahl, S. Beckett and L. O. Mederos (1951) A study of the ankle jerk in myxedema. J. Clin. Endocrin. 11:1186-1205.

Lambert, O. (1965) The relationship between maximum isometric strength and maximum concentric strength at different speeds. Intern. Fed. Phys. Educ. Bull. 35:13.

Lastovka, M. (1969) The conduction velocity of the peripheral motor nerve fibres and physical training. Activ. Nerv. Sup. (Praha) 11:308.

Lautenback, R. and W. W. Tuttle (1932) The relationship between reflex time and running events in track. Res. Quart. 3:136-143.

Lavoie, S., C. Dufresne, C. Vallee and A. W. Taylor (1977) Composition musculaire et surface des fibres chez les femmes et les hommes; effet de l'entrainement. Can. J. Appl. Sport Sci. 2:115-120.

Lawrence, D. G. and S. Locke (1961) Motor nerve conduction velocity in diabetes. Arch. Neurol. 5:483-489.

Lee, R. G. and W. G. Tatton (1975) Motor responses to sudden limb displacements in primates with specific CNS lesions and in human patients with motor systems disorders. Can. J. Neurol. Sci. 2:285-293.

Leister, A. E. (1965) The effect of using the test appartus for training on isometric strength development. Unpublished M.Sc. thesis, Pennsylvania State University.

LeQuesne, P. M. (1971) Nerve conduction in clinical practice. In: Electrodiagnosis and Electromyography. Ed. S. Licht. New Haven, Connecticut: Elizabeth Licht, pp. 419-451.

Lesch, M., W. W. Parmley, M. Hamosh, S. Kaufman and E. Sonneblick (1968) Effects of acute hypertrophy on the contractile properties of skeletal muscle. Am. J. Physiol. 214:685-690.

Less, M., S. E. Krewer and W. W. Eickelberg (1977) Exercise effect on strength and range of motion of hand intrinsic muscles and joints. Arch. Phys. Med. Rehabil. 58:370-374.

Liberson, W. T. and M. M. Asa (1959) Further studies of brief isometric exercises. Arch. Phys. Med. Rehabil. 40:330-336.

Low, M. D., J. V. Basmajian and G. M. Lyons (1962) Conduction velocity and residual latency in the human ulnar nerve and the effects on them of ethyl alcohol. Am. J. Med. Sci. 244:721-730.

Lundervold, A. J. S. (1951) Electromyographic investigations of position and manner of working in typewriting. Acta physiol. scand. 24:Suppl. 84.

McComas, A. J. (1977) Neuromuscular Function and Disorders. London: Butterworths.

McComas, A. J., P. R. W. Fawcett, M. J. Campbell and R. E. P Sica (1971) Electrophysiological estimation of the number of motor units within a human muscle. J. Neurol. Neurosurg. Psychiat. 34:121-131.

McComas, A. J., R. E. P. Sica and S. Banerjee (1978) Long-term effects of partial limb amputation in man. J. Neurol. Neurosurg. Psychiat. 41:425-432.

McComas, A. J., R. E. P. Sica, A. R. McNabb, W. M. Goldberg and A. R. M. Upton (1974) Evidence for reversible motoneurone dysfunction in thyrotoxicosis. *J. Neurol. Neurosurg. Psychiat.* 37:548-558.

McComas, A. J., R. E. P. Sica and F. Petito (1973) Muscle strength in boys of different ages. *J. Neurol. Neurosurg. Psychiat.* 36:171-173.

McComas, A. J. and H. C. Thomas (1968) Fast and slow twitch muscles in man. *J. Neurol. Sci.* 301-307.

MacDougall, J. D., G. Elder, D. G. Sale, J. Moroz and J. R. Sutton (1977a) Skeletal muscle hypertrophy and atrophy with respect to fibre type in humans. *Can. J. Appl. Sport Sci.* 2:229.

MacDougall, J. D., D. G. Sale, G. Elder and J. R. Sutton (1976) Ultrastructural properties of human skeletal muscle following heavy resistance training and immobilization. *Med. Sci. Sports* 8:72.

MacDougall, J. D., D. G. Sale, J. R. Moroz and H. Howald (1978) Mitochordrial volume density in human skeletal muscle following heavy resistance training. *Med. Sci. Sports* 10:56.

MacDougall, J. D., G. R. Ward, D. G. Sale and J. R. Sutton (1977b) Biochemical adaptation of human skeletal muscle to heavy resistance training and immobilization. *J. Appl. Physiol.* 43:700-703.

McIlwain, J. S. and K. C. Hayes (1977) Dynamic properties of human motor units in the Hoffman-reflex and M response. *Am. J. Phys. Med.* 56:122-135.

MacIntosh, D. (1968) Relationship of individual differences and subsequent changes in static strength with speed of forearm flexion movement. *Res. Quart.* 39:138-148.

Mackova, E. and P. Hnik (1971) 'Compensatory' muscle hypertrophy in the rat induced by tenotomy of synergistic muscles. *Experientia* 27:1039-1040.

________ (1973) Compensatory muscle hypertrophy induced by tenotomy of synergists is not true working hypertrophy. *Physiol. bohemcslov.* 22:43-50.

McLeod, J. G. and S. H. Wray (1966) An experimental study of the F wave in the baboon. *J. Neurol. Neurosurg. Psychiat.* 29:196-200.

McMorris, R. O. and E. C. Elkins (1954) A study of production and evaluation of muscular hypertrophy. *Arch. Phys. Med. Rehabil.* 35:420-426.

MacQueen, I. J. (1954) Recent advances in the technique of progressive resistance exercise. *Brit. Med.* J. 2:1193-1198.

Magladery, J. W. and D. B. McDougall (1950) Electrophysiological studies of nerve and reflex activity in normal man. I. Identification of certain reflexes in the electromyogram and the conduction velocity of peripheral nerve fibres. Bull. Johns Hopk. Hosp. 86:265-290.

Magoun, H. W. (1959) Central inhibition and the reticular system. XXI International Congress of Physiological Sciences: Abstracts of communications, pp. 46-49.

Maier, A., J. C. Crockett, D. R. Simpson, S. W. Saubert and V. R. Edgerton (1976) Properties of immobilized guinea pig hind limb muscles. Am. J. Physiol. 231:1520-1526.

Mann, W. S. and B. Salafsky (1970) Enzyme and physiological studies on normal and disused developing fast and slow cat muscles. J. Physiol. 208:33-47.

Mannheimer, J. S. (1969) A comparison of strength gain between concentric and eccentric contractions. Phys. Ther. 49:1201-1207.

Marley, W. P. (1962) The comparative effectiveness of isometric and isotonic exercise in the development of muscular strength, endurance and girth. Unpublished Master's thesis, University of Maryland.

Marsden, C. D. and J. C. Meadows (1970) the effect of adrenaline on the contraction of human muscle. J. Physiol. 207:429-448.

Marsden, C. D., P. A. Merton and H. B. Morton (1976) Stretch reflex and servo action in a variety of human muscles. J. Physiol. 259:531-560.

Mathews, D. K. and R. Kruse (1957) Effects of isometric and isotonic exercises on elbow muscle groups. Res. Quart. 28:26-37.

Mathews, D. K., C. T. Shay, F. Godin and R. Hogdon (1956) Cross transfer effects of training on strength and endurance. Res. Quart. 27:206-212.

Mayer, R. F. and R. G. Feldman (1967) Observations on the nature of the F wave in man. Neurol. (Minneap) 17:147-156.

Melvin, J. L., D. H. Harris and E. W. Johnson (1966) Sensory and motor conduction velocities in the ulnar and median nerves. Arch. Phys. Med. Rehabil. 47:511-519.

Merton, P. A. (1954) Voluntary strength and fatigue. J. Physiol. 123: 553-564.

Messina, C. and R. Cotruto (1976) Different excitability of type 1 and type 2 alpha-motoneurons. The recruitment curve of H- and M-responses in slow and fast muscles of rabbits. J. Neurol. Sci. 28:57-63.

Meyers, C. R. (1967) Effects of two isometric routines on strength, size and endurance in exercised and nonexercised arms. *Res. Quart* 38:430-440.

Michael, L. E. (1963) The effects of isometric contraction exercises on reaction and speed of movement times. Unpublished Doctoral thesis, Louisiana State University.

Milner-Brown, H. S., R. B. Stein and R. G. Lee (1975) Synchronization of human motor units: possible roles of exercise and supraspinal reflexes. *Electroencephalogr. Clin. Neurophysiol*. 38:245-254.

Milner-Brown, H. S., R. B. Stein and R. Yemm (1973) The contractile properties of human motor units during voluntary isometric contractions. *J. Physiol*. 228:285-306.

Moffroid, M. and R. H. Whipple (1970) Specificity of speed of exercise. *Phys. Ther.* 50:1693-1699.

Moffroid, M., R. Whipple, J. Hofkosh, E. Lowman and H. THistle (1969) A study of isokinetic exercise. *Phys. Ther*. 49:735-746.

Moore, J. C. (1975) Excitation overflow: an electromyographic investigation. *Arch. Phys. Med. Rehabil*. 56:115-120.

Morehouse, L. E. (1960) Physiological basis of strength development. In: *Exercise and Fitness*. Chicago: Athletic Institute.

Morehouse, L. E. and A. T. Miller (1976) *Physiology of Exercise.* Saint Louis: C. V. Mosby.

Morrell, F. (1961) Electrophysiological contributions to the neural basis of learning. *Physiol. Rev*. 41:443-494.

Muller, E. A. (1962) Physiology of muscle training. *Rev. Can. Biol*. 21:303-313.

_______ (1970) Influence of training and of inactivity on muscle strength. *Arch. Phys. Med. Rehabil*. 51:449-462.

Nilsson, J., P. Tesch and A. Thorstensson (1977) Fatigue and EMG of repeated fast voluntary contractions in man. *Acta physiol. scand.* 101:194-198.

Norris, A. H., N. W. Shock and I. H. Wagman (1953) Age changes in the maximum conduction velocity of motor fibres of human ulnar nerves. *J. Appl. Physiol*. 5:589-593.

Oku, Y. (1973) Studies on the H reflex induced from human hand muscles. *Electromyogr. Clin. Neurophysiol*. 13:403-431.

Olsen, E. A. (1956) Relationship between psychological capacities and success in college athletics. *Res. Quart.* 27:79-89.

Olson, C. B. and C. P. Swett (1969) Speed of contraction of skeletal muscle. The effect of hypoactivity and hyperactivity. *Arch. Neurol.* 20:263-270.

O'Shea, J. P. (1966) The development of strength and muscle hypertrophy through selected weight programs. *Res. Quart.* 37:95-107.

_______ (1976) *Scientific Principles and Methods of Strength Fitness.* Reading, Massachusetts: Addison-Wesley.

Parker, A. B. (1960) A study of the relationship between reaction time and progressive resistance exercise. Unpublished Master's thesis, Springfield College, Massachusetts.

Patel, A. N., Z. A. Razzak and D. K. Dastur (1969) Disuse atrophy of human skeletal muscles. *Arch. Neurol.* 20:413-421.

Pencek, R. W. (1966) Effects of weight training on body weight, body density and body fat. Unpublished M.Sc. thesis, Pennsylvania State University.

Penman, K. A. (1969) Ultrastructural changes in human striated muscle using three methods of training. *Res. Quart.* 40:764-772.

_______ (1970) Human striated muscle ultrastructural changes accompanying increased strength without hypertrophy. *Res. Quart.* 41:418-424.

Perrine, J. J. (1968) Isokinetic exercise and the mechanical energy potentials of muscle. J. Health Phys. Ed. Rec. 39:40-48.

Perrine, J. J. and V. R. Edgerton (1978) Muscle force-velocity and power velocity relationships under isokinetic loading. *Med. Sci. Sports* 10:159-166.

Person, R. A. and L. P. Kudina (1972) Discharge frequency and discharge pattern of human motor units during voluntary contraction of muscle. *Electroencephal. Clin. Neurophysiol.* 32:471-483.

Peter, J. B., R. J. Barnard, V. R. Edgerton, C. A. Gillespie and K. E. Stempel (1972) Metabolic profiles of three fiber types of skeletal muscle in guinea pig and rabbits. *Biochem.* 11:2627-2633.

Pipes, T. V. and J. H. Wilmore (1975) Isokinetic vs. isotonic strength training in adult men. *Med. Sci. Sports* 7:262-274.

Prince, F. P., R. S. Hikida and F. C. Hagerman (1976) Human muscle fiber types in power lifters, distance runners and untrained subjects. *Pfluegers Arch.* 363:19-26.

Rader, P. (1956) *The Rader Master Bodybuilding and Weight Gaining System.* Alliance, Nebraska: Iron Man Publishing Co.

Radford, P. F. and A. R. M. Upton (1975) Trends in speed of alternated movement during development and among elite springers. In: Biomechanics V-B. Ed. P. V. Komi. Baltimore: University Park Press, pp. 188-193.

Ralston, H. J., B. Feinstein and V. T. Inman (1952) Rate of atrophy in muscles immobilized at different lengths. Fed. Proc. 11:127.

Rasch, P. J. (1954) Relationship of arm-strength, weight and length to speed of movement. Res. Quart. 25:327-332.

________ (1974) The present status of negative (eccentric) exercise: a review. Am. Correct. Ther. J. 28:77-78.

________ (1975) Weight Training. Dubuque, Iowa: Wm. C. Brown.

Rasch, P. J. and C. E. Morehouse (1957) Effect of static and dynamic exercises on muscular strength and hypertrophy. J. Appl. Physiol. 11:29-34.

Reid, J. G. (1967) Static strength increase and its effect upon triceps surae reflex time. Res. Quart. 38:691-697.

Reitsma, W. (1969) Skeletal muscle hypertrophy after heavy exercise in rats with surgically reduced muscle function. Am. J. Phys. Med. 48:237-258.

Retzlaff, E. and J. Fontaine (1965) Functional and structural changes in motor neurons with age. In: Behaviour, Aging and the Nervous System. Ed. A. T. Welford and J. E. Biren. Springfield, Illinois: Charles C. Thomas, pp. 340-352.

Richford, C. (1966) Principles of Successful Bodybuilding. Alliance, Nebraska: Iron Man Magazine.

________ (1968) Lower Body Training. Alliance, Nebraska: Iron Man Magazine.

Rodgers, K. L. and R. A. Berger (1974) Motor-unit involvement and tension during maximum, voluntary concentric, eccentric and isometric contractions of the elbow flexors. Med. Sci. Sports 6:253-259.

Rose, D. L., S. F. Radzyminski and R. R. Beatty (1957) Effect of brief maximal exercise on strength of the quadriceps femoris. Arch. Phys. Med. Rehabil. 38:157-164.

Roush, E. S. (1951) Strength and endurance in the waking and hypnotic state. J. Appl. Physiol. 3:404-410.

[redacted], R. W. D. (1969) The effect of hypertrophy on the properties of skeletal muscle. Comp. Biochem. Physiol. 28:1449-1453.

Rowe, R. W. D. and G. Goldspink (1968) Surgically induced hypertrophy in skeletal muscles of the laboratory mouse. Anat. Rec. 161:69-76.

Sammeck, R. (1975) Training-induced myelination in peripheral nerves of the rat. J. Physiol. 244:7P.

Samorajski, T. and C. Rolsten (1975) Nerve fiber hypertrophy in posterior tibial nerves of mice in response to voluntary running activity during aging. J. Comp. Neurol. 159:553-558.

Sanders, F. K. and D. J. Whitteridge (1946) Conduction velocity and myelin thickness in regenerating nerve fiber. J. Physiol. 105: 152-174.

Sargeant, A. J. and C. T. M. Davies (1977) The effect of disuse muscular atrophy on the forces generated in dynamic exercise. Clin. Sci. Mol. Med. 53:183-188.

Sargeant, A. J., C. T. M. Davies, R. H. T. Edwards, C. Maunder and A. Young (1977) Functional and structural changes after disuse of human muscle. Clin. Sci. Mol. Med. 52:337-342.

Schiaffino, S. and V. Hanzlikova (1970) On the mechanism of compensatory hypertrophy in skeletal muscles. Experientia 26:152.

Secher, N. H. (1975) Isometric rowing strength of experienced and unexperienced oarsmen. Med. Sci. Sports 7:280-283.

Secher, N. H., S. Rorsgaard and O. Secher (1977) Contralateral influence on recruitment of curarized muscle fibres during maximal voluntary extension of the legs. VIth Int. Congr. Biomechanics, Copenhagen.

Seiden, D. (1976) Quantitative analysis of muscle cell changes in compensatory hypertrophy and work-induced hypertrophy. Am. J. Anat. 145:459-465.

Sharpless, S. K. (1964) Reorganization of function in the nervous system--use and disuse. Ann. Rev. Physiol. 26:357-388.

Sica, R. E. P. and A. J. McComas (1971) Fast and slow twitch units in a human muscle. J. Neurol. Neurosurg. Psychiat. 34:113-120.

________ (1978) The neural hypothesis of muscular dystrophy. A review of recent experimental evidence with particular reference to the Duchenne form. Can. J. Neurol. Sci. 5:189-197.

Sica, R. E. P., A. J. McComas and A. R. M. Upton (1971) Impaired potentiation of H-reflexes in patients with upper motoneurone lesions. J. Neurol. Neurosurg. Psychiat. 34:712-717.

Sica, R. E. P., A. J. McComas, A. R. M. Upton and D. Longmire (1974) Motor unit estimations in small muscles of the hand. J. Neurol. Neurosurg. Psychiat. 37:55-67.

Sills, F. D. and A. L. Olson (1958) Action potentials in unexercised arm when opposite arm is exercised. Res. Quart. 29:213-221.

Simonsen, E. (1971) Physiology of Work Capacity and Fatigue. Springfield, Illinois: Charles C. Thomas.

Slater-Hammel, T. A. (1950) Bilateral effects of muscular activity. Res. Quart. 21:203-209.

Slater-Hammel, A. T. (1955) Comparisons of reaction-time measures to a visual stimulus and arm movement. Res. Quart. 26:470-479.

Slomic, A., R. Rosefalck and F. Buchtal (1968) Electrical and mechanical responses of normal and myasthenic muscle. Brain Res. 10:1-78.

Smith, L. E. (1969) Specificity of individual differences of relationships between forearm 'strengths' and speed of forearm flexion. Res. Quart. 40:191-197.

Smorto, M. P. and J. V. Basmajian (1972) Clinical Electroneurography. Baltimore: Williams and Wilkins.

Snyder, D. H., D. H. Rifenberick and S. R. Max (1973) Effects of neuromuscular activity on choline acetyltransferase and acetylcholinesterase. Exp. Neurol. 40:36-42.

Sola, O. M., D. L. Christensen and A. W. Martin (1973) Hypertrophy and hyperplasia of adult chicken anterior latissimus dorsi muscles following stretch with and without denervation. Exp. Neurol. 41:76-100.

Staudte, H. W., G. U. Exner and D. Pette (1973) Effects of short-term, high intensity (sprint) training on some contractile and metabolic characteristics of fast and slow muscle of the rat. Pfluegers Archiv. 344:159-168.

Steiner, B. J. (1974) Complete Guide to Effective Barbell Training. Alliance, Nebraska: Iron Man Industries.

Stephens, J. A. and T. P. Usherwood (1975) The fatigability of human motor units. J. Physiol. 250:37P-38P.

Stillwell, D. M., G. L. McLarren and J. W. Gersten (1967) Atrophy of quadriceps muscle due to immobilization of the lower extremity. Arch. Phys. Med. Rehabil. 48:289-295.

Stish, E. V. (1958) Electromyographic study of the contralateral effects of the biceps brachii. Unpublished Ph.D. thesis, State University of Iowa.

Stothart, J. P. (1973) Relationship between selected biomechanical parameters of static and dynamic muscle performance. Biomechanics III. Basel: Karger, pp. 210-217.

Stromme, S. B., H. D. Meen and A. Aakuaag (1974) Effects of an androgenic-anabolic steroid on strength development and plasma testosterone levels in normal males. Med. Sci. Sports 6:203-208.

Summers, T. B. and H. M. Hines (1951) Effect of immobilization in various positions upon the strength and weight of skeletal muscle. Arch. Phys. Med. Rehabil. 32:142-145.

Sunderland, S. (1968) Nerves and Nerve Injuries. London: E. & S. Livingstone.

Tabary, J. C., C. Tabary, C. Tardieu, G. Tardieu and G. Goldspink (1972) Physiological and structural changes in the cat's soleus muscle due to immobilization at different lengths by plaster casts. J. Physiol. 224:231-244.

Takamori, M., L. Gutmann and S. R. Shane (1971) Contractile properties of human skeletal muscle. Arch. Neurol. 25:535-546.

Tanner, J. M. (1952) The effect of weight lifting on physique. Am. J. Phys. Anthrop. 10:427-461.

Teasdale, R. D., A. M. Park, H. W. Languth and J. W. Magladery (1952) Electrophysiological studies of reflex activity in patients with lesions of the nervous system. II Disclosure of normally suppressed monosynaptic reflex discharge of spinal motoneurones by lesions of lower brain-stem and spinal cord. Bull. Johns Hopk. Hosp. 91:245-256.

Tesch, P. and J. Karlsson (1970) Isometric strength performance and muscle fibre type distribtuion in man. Acta physiol. scand. 103:47-51.

Thistle, H. G., H. J. Hislop, M. Moffroid and E. W. Lowman (1967) Ioskinetic contraction: A new concept of resistance exercise. Arch. Phys. Med. Rehabil. 48:279-282.

Thomas, J. E. and E. H. Lambert (1960) Ulnar nerve conduction velocity and H-reflex in infants and children. J. Appl. Physiol. 15:1-9.

Thomas, P. K., T. A. Sears and R. W. Gilliatt (1959) The range of conduction velocity in normal motor nerve fibres to the small muscles of the hand and foot. J. Neurol. Neurosurg. Psychiat. 22:175-181.

Thompson, T. C. (1934) Experimental muscular atrophy. J. Bone Joint Surg. 16:564-571.

Thomsen, P. and J. V. Luco (1944) Changes of weight and neuromuscular transmission in muscles of immobilized joints. J. Neurophysiol. 7:245-251.

Thorne, J. (1965) Central responses to electrical activation of the peripheral nerves supplying the intrinsic hand muscles. J. Neurol. Neurosurg. Psychiat. 28:482-495.

Thorstensson, A. (1976) Muscle strength, fibre types and enzyme activities in man. Acta physiol. scand. Suppl. 443.

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

Thorstensson, A., B. Hulten, W. von Doblen and J. Karlsson (1976b) Effect of strength training on enzyme activities and fibre characteristics in human skeletal muscle. Acta physiol. scand. 96:392-398.

Thorstensson, A., and J. Karlsson (1976) Fatiguability and fibre composition of human skeletal muscle. Acta physiol. scand. 98:318-322.

Thorstensson, A., L. Larson, P. Tesch and J. Karlsson (1977) Muscle strength and fiber composition in athletes and sedentary men. Med. Sci. Sports 9:26-30.

Thorstensson, A., B. Sjodin and J. Karlsson (1975) Enzyme activities and muscle strength after 'sprint training' in man. Acta physiol. scand. 94:313-318.

Tipton, C. M. and P. V. Karpovich (1966) Exercise and the patellar reflex. J. Appl. Physiol. 21:15-18.

Tomanek, R. J. (1968) Limb immobilization and the diameters and number of nerve fibers. J. Comp. Neurol. 134:477-484.

Tomanek, R. J. and D. D. Lund (1974) Degeneration of different types of skeletal muscle fibres. II Immobilization. J. Anat. 118:531-541.

Tomanek, R. J. and C. M. Tipton (1967) Influence of exercise and tenectomy on the morphology of a muscle nerve. Anat. Rec. 159:105-114.

Tornvall, G. (1963) Assessment of physical capabilities. Acta physiol. scand. Suppl. 201.

Trojaborg, W. (1964) Motor nerve conduction velocities in normal subjects with particular reference to the conduction in proximal and distal segments of median and ulnar nerve. Electroenceph. Clin Neurophysiol. 17:314-321.

Upton, A. R. M., A. J. McComas and R. E. P. Sica (1971) Potentiation of 'late' responses evoked in muscles during effort. J. Neurol. Neurosurg. Psychiat. 34:699-711.

Upton, A. R. M. and P. F. Radford (1975) Motoneurone excitability in elite sprinters. In: Biomechanics V-A. Ed. P. V. Komi. Baltimore: University Park Press, pp. 82-87.

Van Linge, B. (1962) The response of muscle to strenuous exercise. J. Bone Joint Surg. 44-B:711-721.

Vrbova, G. (1963) The effect of motoneurone activity on the speed of contraction of striated muscle. J. Physiol. 169:513-526.

Wagnar, L. E. (1970) The effect of isokinetic exercise on the transfer of strength to the contralateral arm. Unpublished M. Ed. thesis, East Stroudsburg State College.

Ward, J. and C. H. Fisk (1964) The difference in response of the quadriceps and the biceps brachialis muscles. Arch. Phys. Med. Rehabil. 45:614-620.

Ward, P. E. (1963) The effects of isometric and isotonic exercises on strength, endurance and anthropometric measurements. Unpublished M.Sc. thesis, University of Washington.

Warmolts, J. R. and W. K. Engel (1972) Open-biopsy electromyography. Arch. Neurol. 27:512-517.

Weaver, R. A., W. M. Landau, J. F. Higgins (1963) Fusimotor function. Part II. Evidence of fusimotor depression in human spinal shock. Arch. Neurol. 9:127-132.

Wells, J. B. (1969) Functional integrity of rat muscle after isometric immobilization. Exp. Neurol. 24:514-522.

Westerland, S. H. and W. W. Tuttle (1931) The relationship between running events in track and reaction time. Res. Quart. 2:95-100.

Whitley, J. D. and G. Elliott (1968) Learning component of repetitive maximal static contractions. Percept. Mot. Skills 27:1195-1200.

Whitley, J. D. and L. E. Smith (1963) Velocity curves and static strength-action strength correlations in relation to the mass moved by the arm. Res. Quart. 34:379-395.

Wilkie, D. R. (1950) The relation between force and velocity in human muscle. J. Physiol. 110:249-260.

Willems, E. J. (1973) The relationship between the rate of tension development and the strength of a voluntary isometric muscular contraction in man. In: Biomechanics III. Basel: Karger, pp. 218-223.

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

Woo, S. L., J. V. Matthews, W. H. Akeson, D. Amiel and F. R. Convery (1975) Connective tissue response to immobility. Correlative study of biomechanical and biochemical measurements of normal and immobilized rabbit knees. Arthritis Rheum. 18:257-264.

Wright, V. and R. J. Johns (1960a) Physical factors concerned with the stiffness of normal and diseased joints. Bull. Johns. Hopk. Hosp. 106:215-231.

_______ (1960b) Observations on the measurement of joint stiffness. Arthritis Rheum. 3:328-340.

Yougen, L. (1959) A comparison of reaction time and movement times of women athletes and non-athletes. Res. Quart. 30:349-355.

DEFINITION OF TERMS

average power The work done by a maximal concentric contraction divided by the duration of the contraction. Units are Watts (W; 1 W = 1 J/s). See also p. 58.

average torque The impulse developed by a maximal concentric contraction divided by the duration of the contraction. Units are newton-metres (N.m). See also p. 58.

compensatory hypertrophy (CH) An experimental technique whereby a muscle is functionally overloaded by functional removal of its synergists. See also p. 13.

concentric contraction The muscle shortens while producing force; that is, the muscle force exceeds the resisting force.

contraction The muscle attempts to shorten while producing force; whether the muscle shortens, lengthens or remains the same length depends upon the magnitude of the resisting force.

contraction time The time between the beginning of a twitch contraction and the point when the twitch tension is maximal (i.e. time to peak tension). See also p. 73.

eccentric contraction The muscle lengthens while producing force; that is, the resisting force exceeds the muscle force.

endurance training Consists of sustained or repeated muscle contractions at a low percentage of maximal contraction force; referred to as low resistance, high repetition training.

half relaxation time The period of time during the relaxation phase of a muscle twitch contraction in which the tension decreases to one half of the maximal tension attained during the contraction. See also p. 73.

<u>immobilization</u> A method of inducing relative hypoactivity of a muscle group; consists of restricting joint movement by means of a cast. See also p. 78.

<u>impulse</u> The average torque developed during a concentric contraction multiplied by the duration of the contraction. Units are newton-metre-seconds (N.m.s)

<u>isokinetic contraction</u> A muscle contraction performed at constant velocity of shortening (concentric) or lengthening (eccentric). An isometric contraction is a special case of isokinetic contraction, in which the velocity is zero. See also p. 5.

<u>isometric contraction</u> The muscle remains the same length while producing force; that is, the muscle force is equal to the resisting force. See also p. 4.

<u>isotonic contraction</u> A concentric contraction of constant force throughout its duration. See also p. 4.

<u>method error</u> A method for indicating the reproducibility of measurements. See also p. 90.

<u>motor unit count</u> An estimate of the number of motor units within a muscle. See also p. 61.

<u>M wave</u> The electromyographically recorded response of a muscle evoked by supra maximal nerve stimulation.

<u>peak power</u> The peak torque developed during a maximal concentric contraction multiplied by the velocity (joint angular velocity) of contraction. Units are watts (W).

<u>peak torque</u> The maximum torque developed during a maximal concentric contraction. Units are newton-metres (N.m).

<u>rate of tension development</u> The peak tension attained by a muscle twitch contraction divided by the contraction time of the twitch. Units are newtons/second (N/s). See also p. 73.

<u>reflex potentiation</u> The potentiation, by voluntary muscle contraction, of the electromyographically recorded reflex responses evoked by supra maximal nerve stimulation. See also p. 65.

sprint training Running or swimming training at maximal or near maximal velocity. See also p. 25.

strength training Training which consists of maximal or near maximal muscle contractions; also called high resistance, low repetition exercise. See also p. 4.

strength-velocity relation ratio High velocity strength (peak torque, average torque, impulse, work, peak power, average power) performance divided by low velocity strength performance. See also p. 61.

symmetry ratio For any measure mode on both left and right sides, the lesser value divided by the greater value.

V (coefficient of variation) The method error, or standard deviation, expressed as a percentage of the mean.

voluntary strength The mechanical effects of a maximal voluntary muscle contraction. See also p. 1.

V_1 ratio The amplitude of the V_1 wave divided by the amplitude of the maximum M wave. See also p. 65.

V_2 ratio The amplitude of the V_2 wave divided by the amplitude of the maximum M wave. See also p. 65.

work The average torque developed during a maximal concentric contraction multiplied by the displacement through which the torque acted. Units are joules (J).