AGING AND HUMAN NEUROMUSCULAR FUNCTION

BY

ANTHONY ALLAN VANDERVOORT, B. Sc., M. Sc.

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AUTHOR: Anthony Allan Vandervoort, B. Sc. (University of Waterloo)

M. Sc. (McMaster University)

SUPERVISOR: Professor Alan J. McComas

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ABSTRACT

In view of the importance of maintaining normal mobility in the aging population, the function of two opposing groups of leg muscles, the ankle dorsiflexors and plantarflexors, was studied in a sample of 111 healthy men and women aged 20 to 100 yr. Three major questions were asked in this investigation: (1) To what extent does muscle strength decline with age? (2) Can descending motor pathways be optimally utilized by the elderly for activating lower motor neurons? (3) Does the time-course of muscle contraction become prolonged with age?

Summarized results were:

1. Maximal voluntary isometric strength (MVC) of the dorsiflexor and plantarflexor muscles showed a general pattern of decreased values after the fifth decade in both sexes. A similar decline of approximately 13% per decade was observed in the two muscle groups. As the plantarflexor muscles produced 4 times more torque than the dorsiflexor muscles in young adults, the absolute loss of strength was much greater for plantarflexor MVC.

2. The majority of subjects at all ages were able to utilize their descending motor pathways optimally for full muscle activation.

3. Contraction time and one-half relaxation time of the isometric twitch were prolonged with increased age in both muscles.

4. An additional observation was that flexibility of the ankle joint was reduced with increased age, although considerable rotation of the ankle was still possible in the oldest subjects.

Evidence from analysis of the compound muscle action potentials,

peak twitch torques and muscle cross-sectional areas supported the conclusion that the decrease in strength with aging was due to a loss of excitable muscle mass. It was hypothesized that fat and connective tissue replaced muscle in the elderly. The findings of this study add to our knowledge about the aging process and its influence on neuromuscular function. It is also anticipated the results will be useful in geriatric clinics and for planning programs aimed at the prevention and rehabilitation of neuromuscular disability in the elderly population.

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LIST OF ABBREVIATIONS

Ach	= acetylcholine
C	= Centigrade
Ca^{2+}	= calcium ion
cm	= centimetre
CSA	= cross-sectional area
CT	= contraction time of the isometric muscle twitch
D	= dorsiflexion (direction of ankle joint rotation)
DF	= dorsiflexor (muscle group)
EDB	= extensor digitorum brevis
EDL	= extensor digitorum longus
EMG	= electromyogram
e.p.p.	= end-plate potential
Hz	= hertz (cycles per second)
kg	= kilogram
LG	= lateral gastrocnemius
m.e.p.p.	= miniature end-plate potential
MG	= medial gastrocnemius
ms	= millisecond
Mv	= millivolt
MVC	= maximal voluntary contraction
M-wave	= compound muscle action potential
N.m	= Newton metre
NMJ	= neuromuscular junction
P	= plantarflexion (direction of ankle rotation)
PF	= plantarflexor (muscle group)
P_t	= peak torque level of the isometric muscle twitch
r	= Pearson product moment correlation
s	= seconds
SD	= standard deviation
SOL	= soleus
yr	= year
o	= degree
$\bar{x}$	= mean
1/2 RT	= one-half relaxation time of the isometric muscle twitch

I. INTRODUCTION

A. Purpose and Scope of the Investigation

Normal mobility is a sign of health in old age. Despite the importance of maintaining muscle strength and joint flexibility in the legs of the elderly, there is a lack of comprehensive research regarding the effects of aging on these parameters. Most studies have been limited to one muscle group and usually only men were tested. The muscles which act at the ankle joint as integral components of normal balance and walking activity have not been examined in persons over the age of 70 years (yr). Controversy exists in the literature about the issues of when in adult life muscle strength begins to decline and why.

The aims of this study were to answer the following questions:

1. What is the relationship between aging and strength of muscles acting at the ankle joint in adult men and women?
2. Can descending motor pathways be optimally utilized for muscle activation by the aged individual?
3. Does the time-course of muscle contraction become prolonged with aging?

This study was confined to the opposing muscle groups that act on the ankle, producing dorsiflexion and plantarflexion respectively. Healthy adult men and women between the ages of 20 and 100 yr of age participated in the neuromuscular function testing program. All subjects were living independently in the community and were able to walk without physical aid.

B. Review of Literature

Changes in Human Muscle Strength with Aging

A decrease in muscle strength has often been reported as a characteristic of human aging. The phenomenon of weakness in old age has received attention since at least the middle 1800's when Quetelet (1835) reported his observations on back and hand strength of men and women as old as 60 yr of age (quoted in Fisher and Birren, 1947). Unfortunately, numbers and characteristics of subjects were seldom reported in these early studies.

In more recent investigations, individuals of various ages have been compared with regard to their strength in maximal voluntary contractions (MVCs). Several muscle groups from the upper and lower limb have been examined. Table 1 summarizes studies of adults at least as old as the seventh decade with regard to changes in isometric strength with aging (isometric refers to constant muscle length). Six muscle groups have been compared: ankle plantarflexors, ankle dorsiflexors, knee extensors, knee flexors, elbow flexors and handgrip. Several generalizations can be made from an analysis of the results.

First, there is no clear-cut difference in the effects of aging between distal and proximal muscles, or between muscles of the upper and lower limbs. For example, in the study by Potvin et al.(1980), the decline in MVC observed for handgrip with increasing age was exactly the same as for ankle dorsiflexion. But McDonagh et al. (1984) recently reported a greater reduction in plantarflexor strength than in

Table 1. Summary of Literature on Changes in Muscle Strength with Aging

Study	Muscle Action	Sex	Oldest Age Group	N	% Decline in Strength vs Young Adults	Mean Difference in Size vs Young Adults Height (cm)	Weight (kg)
	ANKLE						
1.	Plantar-flexion	M	60-65	8	21	-4	+9
		F	60-65	7	24	-2	+11
2.	"	M	$\bar{x}$= 69	9	43	-13	+0.2
3.	Dorsiflex.	M	70-80	10	20	Not Reported	
	KNEE						
4.	Extension	M	60-69	16	25	-7.5	-4.5
5.	"	M	70-86	24	45	Not Reported	
6.	"	M	55-73	15	39	+2.2	+3.9
7.	"	F	50-80	15	40	Not Reported	
5.	Flexion	M	70-86	24	36	Not Reported	
	HAND						
8.	Handgrip	M	53-68	20	17	Not Reported	
9.	"	M	75-79	4	38	Not Reported	
10.	"	M	60-69	10	18	Not Reported	
11.	"	M	53-64	19	28	0	+8.5
11.	"	F	60-66	6	37	-0.5	-0.8
12.	"	M	51-62	27	3	-1.9	+6.4
13.	"	F	50-65	22	28	-6.8	0
3.	"	M	70-80	10	20	Not Reported	
14.	"	M	60-90	30-40	47	Not Reported	
14.	"	F	60-90	"	42	Not Reported	
	ELBOW						
15.	Flexion	M	67-72	5	31	Not Reported	
16.	"	M	$\bar{x}$= 71	11	20	-4	+9

Authors: 1. Fugl-Meyer et al. (1980) 2. Davies et al. (1983) 3. Potvin et al. (1980) 4. Larsson et al. (1979) 5. Murray et al. (1980) 6. Clarkson et al. (1981) 7. Johnson (1982) 8. Fisher and Birren (1947) 9. Burke et al. (1953) 10. Shephard (1969) 11. Asmussen et al. (1975) 12. Petrofsky and Lind (1975) 13. Petrofsky et al. (1975) 14. Agnew and Maas (1982) 15. Moritani and deVries (1980) 16. McDonagh et al. (1984)

elbow strength when a group of 4 men, aged approximately 70 yr, were compared to young men (average difference was 41% for the ankle muscles vs 20% for the arm muscles). Customary activity could be an important factor in these types of muscle group comparisons and it is noteworthy that the old men tested in Davies laboratory by McDonagh and co-workers were retired manual industrial workers. Second, males and females appear to experience similar aging changes, although research on women has been limited. A third observation is that by the seventh decade average MVC is at least 20% lower than in young adults (20-30 yr olds). It should be noted that all studies but one used a cross-sectional examination of the aging population as the research design, but the longitudinal study of Asmussen et al. (1975) tends to confirm the cross-sectional observations of the other investigators.

There are several criticisms to be made of these studies. First, there has not always been adequate consideration for size differences between young and old adults. Muscle strength is positively correlated to body size (Lamphiear and Montoye, 1976; O'Donovan and Watson, 1977), presumably because of differences in cross-sectional muscle area and in lever arm. Thus, where differences in size exist, it is not clear how much of the apparent aging effect on MVC was attributable to this factor. In some of the studies cited in Table 1 information on size was not reported.

Small numbers of subjects have been studied in some cases, particularly with advanced aged groups (e.g. Burke et al., 1953). Other investigators have grouped several decades of age into one category, thereby masking the aging effect (e.g. Agnew and Mass, 1982). Most of the studies have lacked representatives of the elderly

population over 80 yr of age and in some cases the oldest subject was only in the sixties. Females have been examined in few of the investigations. Not all studies have reported whether there was any assessment or matching of daily activity patterns among the various age groups, despite the knowledge that muscle strength can be strikingly altered by "overload" resistance training or prolonged inactivity (Sale et al., 1982).

There is a further methodological criticism which can be raised with all of the studies employing measurements of maximal voluntary strength. A MVC requires the subject to make an intense mental effort, and it is not clear how much of the difference between young and old subjects can be attributed to lesser motivation on the part of the latter. Maximum isometric muscle contraction can involve brief discomfort due to several factors, such as internal muscle sensation, pressure on the skin and joints, and chafing against the straps and restraints of the measurement device. Also, some people may have an emotional unwillingness to be physically forceful (Ikai and Steinhaus, 1961). Fortunately, this last factor can be evaluated by using the twitch interpolation technique of Belanger and McComas (1981). With this method, during the voluntary effort of a subject an attempt is made to produce an involuntary muscle twitch by electrical stimulation of the appropriate motor nerve. This technique allows an assessment of the extent to which the individual has activated the musculature with his/her volition. If full voluntary activation has been achieved the stimulus adds nothing more.

Muscle strength can also be evaluated by tetanically stimulating the appropriate motor nerve and comparing this output to the MVC.

Unfortunately, antagonistic muscle groups may be excited by the tetanic stimulus and contaminate the force record. This procedure is painful when sufficiently high current to cause maximal muscle contraction is used. Rupture of muscle and tendons is also a possibility in frail subjects. Thus, while some investigators have used tetanic stimulation in their testing protocol (e.g. Davies et al., 1983), subject selection was biased towards highly-motivated people who would submit to the procedure. Only a few of the subjects tolerated tetanizing current in McDonagh et al.'s (1984) study and it appears that this form of muscle stimulation would not be suitable for a large survey of volunteers from the community.

In only one of the studies summarized in Table 1 were the agonists and antagonists acting at a joint compared to determine if a differential effect of aging was present. Murray et al. (1980) found a slightly greater decline in the strength of knee extensors than in that of knee flexors. These results were of added interest in that one of the muscle groups, the knee extensors, had an "anti-gravity" role. Is there a critical level of strength required in the extensors for normal mobility? Such an analysis is also relevant to the muscles acting at the ankle joint which are involved in maintenance of the upright posture and in locomotion. Even during walking, the anti-gravity plantarflexors are known to produce substantial torques (Winter, 1981).

The question arises whether the relationship between muscle strength and age is linear or curvilinear throughout the adult years. After post-pubertal increases in strength, which are particularly striking in the male (Tanner, 1978; Shephard, 1982), the relationship between MVC and age has been found to plateau for at least 30 yr in

many studies. This plateau has been observed for muscles of the upper limb (Shephard, 1969; Shock and Norris, 1970; Petrofsky and Lind, 1975; Montoye and Lamphiear, 1977; Agnew and Maas, 1982) and for muscles of the lower limb (Larsson et al., 1979; Fugl-Meyer et al., 1980; Belanger et al., 1983). Other investigators have reported a gradual linear decline in MVC after about 30 yr of age (Fisher and Birren, 1947; Burke et al., 1953; Asmussen and Heeboll-Nielsen, 1961, as quoted in Asmussen, 1980; Asmussen et al., 1975; Petrofsky et al., 1975, for women).

Summary. Most research supports the conclusion that there is little change in adult strength until the sixth or seventh decades. The concept of a linear decline in muscle function with age, popularized by Shock in a Scientific American article in 1962, is at best fragile and cannot be generalized to all muscle groups. Linear correlations between MVC and age in the range of 20 to 60-70 yr have been very low in terms of predictive value. The one longitudinal study cited provided an observation that handgrip strength decreased by an average of 20% between the ages of 24 and 50 (Asmussen et al., 1975). It should be noted that when first examined, these subjects were physical education students with high activity and fitness levels. According to measures of exercise capacity, this activity pattern was not maintained into middle age. Decreases in activity level due to altered lifestyles may have therefore exaggerated the apparent effect of aging.

Basis for Decline in Maximum Voluntary Strength with Aging

Several alternative explanations may be advanced for the diminished strength observed in the elderly. In cross-sectional studies, there may be extraneous factors such as body size and habitual activity levels that differ between age groups. However, the age effect persisted when these factors were eliminated, either by matching groups on the variables or by using statistical analyses that allowed for control of group differences (e.g. Petrofsky and Lind, 1975a; Clarkson et al., 1981; Johnson, 1982). The conclusion from these studies was that the older subjects had less muscle capacity for tension generation and/or older subjects were not performing optimally when asked to make maximum efforts. The latter possibility has not been adequately evaluated to date, as discussed previously in the literature review.

With regard to the first possibility, muscle tissue seems to be lost with advancing age, according to investigations on the body composition of elderly individuals. A variety of assessment techniques have been used in this research. Whole body examinations of non-fat tissue proportions have been generated from anthropometric measurements such as densitometry, potassium-40 scanning or simply measuring skinfold thickness. While a number of studies in which these methods were used have reported a loss of lean body mass with aging (Forbes and Reina, 1970; Parizikova et al., 1971; Steen et al., 1977; MacLennan et al., 1980; Dill et al., 1982), it was not clear how much of this was due to loss of muscle mass or to loss of other fat-free tissue. Tzankoff and Norris (1977) estimated total muscle mass specifically by

measuring 24 hour creatinine clearance. Their oldest 12 men, with a mean age of 90, showed on average a 45% reduction in muscle mass compared with mature young adults. The group of men with a mean age of 50 showed only a 7% loss.

There are drawbacks to these whole-body studies. In all cases, an index of lean body or muscle mass was derived from predictor variables, such as creatinine clearance, rather than by measuring the muscle tissue itself. Additionally, differences in loss among individual muscle groups could not be determined. An alternative has been to compare the sizes of specific muscle groups in young and old subjects, using either radiographic imaging or cadervic material.

Recently, the technique of computerized axial tomography (CAT-Scan) has been applied to the problem of measuring muscle mass in the elderly. Borkan et al. (1983) have shown that men aged 59 to 76 yr (mean=69.4 yr) had, on average, 12.4% less muscle cross-sectional area (CSA) in the upper leg and 11.7% less in the upper arm, when compared to a group of middle-aged men. This loss was virtually the same as the total loss of lean body mass (as determined by potassium-40 scanning). However, the loss of muscle cross-sectional area in the chest region was only 2%. Ultrasonic imaging of limbs has been promoted by Young et al. (1980) as a practical, alternative method to the elaborate CAT-Scan equipment; they initially demonstrated that the technique can be used to accurately assess quadriceps muscle wasting following plaster cast immobilization of the knee joint. They have also reported smaller quadriceps CSAs in old men and women as compared to young adults (Young et al., 1982; Stokes et al., 1983).

Muscle Histology

Is the loss of muscle mass with aging due to a reduction in the total number of fibres and/or due to a shrinkage in the sizes of individual fibres? Muscle biopsies have been taken from healthy, elderly individuals in an attempt to answer this question. Larsson et al. (1979) reported that their sample of 60-65 yr old men had smaller vastus lateralis (VL) muscle fibres than young men. This was true for both the Type I and Type II muscle fibre types (Note : Type I and Type II refer to staining characteristics of the myosin ATPase present in the muscle fibre: whether it is acid stable or alkaline stable; see Engel (1962). Three basic fibre types are now recognized, Type I, Type IIa, and Type IIB (Brooke and Kaiser, 1970), and this terminology is used in the present study. These three types generally correspond to the classification scheme of Peter et al. (1972) based on functional properties: slow-twitch oxidative (SO) fibres, fast-twitch oxidative-glycolytic (FOG) fibres and fast-twitch glycolytic (FG) fibres. Garnett et al. (1979) have demonstrated that fibres of the human medial gastrocnemius muscle which stained histochemically as Type I, Type II, and Type IIB exhibited physiological characteristics consistent with the SO, FOG, FG classification scheme. However, these authors and others (see Burke, 1981) have also noted that considerable variation in twitch speed, capacity for post-tetanic potentiation, and fatiguability exists in each fibre type category).

Larsson et al. (1979) found the average Type II fibre diameter was reduced by 42% in their older men, as compared to a 23% change in the

Type I fibres. As well, it appeared that some Type II fibres had been lost from old muscles because there was a lower percentage of the Type II fibres in the aging VL. A co-author in the Larsson investigation, Grimby, has since been involved in another study of aging VL muscles in which Type I fibre size was not decreased in 80 yr old men and women, although Type II size was (Grimby et al., 1982). Furthermore, these authors found no change in the proportions of Type II and Type I fibres in the muscle. Aniansson et al. (1981) reported no change in fibre size with aging in men and women aged 67 to 76, except for the Type IIB fibres. Larsson (1983) however, has criticized the work of Grimby et al. (1982) for the inclusion of persons with disease in their sample and for their histological methods in which rather small biopsies were obtained. Larsson quoted other data of Scelsi et al. (1980) on 65 to 89 yr olds, which confirmed his observations of a Type II muscle fibre atrophy relative to Type I in the vastus lateralis with aging (Larsson, 1983). Other investigators have also reported this as characteristic of old human muscle (Tomonaga, 1977; Clarkson et al., 1981).

The technique of predicting an entire muscle's characteristics from a single biopsy which is only a few millimeters square could lead to erroneous conclusions (Elder et al., 1982; Nygaard and Sanchez, 1982). In an alternative approach, the entire vastus lateralis was removed from young and old (70 to 73 yr) men who were apparently in good health before sudden, accidental death (Lexell et al., 1983). A slice through the mid-section of VL was obtained and then analyzed at many different sites for fibre type distribution and size. On average, the older men had 24% fewer muscle fibres, but there was no significant change in fibre type distribution or fibre size. Grimby and Saltin

(1983) also reported a similar finding of no change in the mean size of elderly soleus muscle fibres. Lexell et al. (1983) noted that variability between subjects was greater in the elderly, and this has been reported in other cadaveric studies (Tomlinson et al., 1969; Jennekens et al., 1971). Therefore, the generalization that "preferential Type II muscle fibre atrophy occurs with aging" is questionable.

Electrophysiological Investigations of Lower Leg Muscles

Muscles below the knee have not been studied as extensively as the quadriceps with regard to muscle histology and aging, but more detailed physiological data is available for the former. Campbell et al. (1973) observed that the size of the isometric twitch of the extensor hallucis brevis muscle was lower in a group of healthy old men and women, as compared to young controls. In addition, the contraction time of the twitch was found to be prolonged and compound muscle action potentials recorded from the extensor digitorum brevis (EDB) muscle were reduced in the elderly. These observations, combined with the demonstration of a decrease in the maximal impulse conduction velocity of the motor nerves and a decrease in the number of motor units in the EDB muscle with aging, suggested that some Type II motor units had been lost. Alternatively, some Type II units may have become more like Type I units with aging, thereby leading to a slower rate of muscle tension development.

Davies et al. (1983) have reported that the plantarflexor muscles also had prolonged twitches in older men (all aged close to 69 yr), as

compared to young adults. The peak twitch torque was lower in the older men as well. Belanger et al. (1983) have confirmed in both men and women that the plantarflexor twitch is prolonged in older individuals. The antagonist dorsiflexor muscle, tibialis anterior, did not show this effect in the age range studied (20-65 yr). No decrease in peak twitch torque with advancing age was observed in either muscle by Belanger et al. (1983).

Isometric twitch analysis. It should be noted that the time-course of the isometric twitch is governed by several factors including (cf. Close, 1972; Carlson and Wilkie, 1974; Blinks et al., 1978) :

(1) the regulation of the "active state" (Hill, 1949) period of tension generation by the myofilaments. The calcium (Ca) controlling apparatus, the sarcoplasmic reticulum and the cytoplasmic proteins that bind free Ca^{2+} ions, regulate this period because Ca^{2+} binding to troponin releases the inhibitory influence of the latter on actin-myosin interactions.

(2) the type of myosin present: whether it is Type I or Type II, based on myosin ATPase staining.

(3) the stiffness of the series elastic component, which transmits the contractile force across the joint.

With regard to Ca^{2+} regulation, Kugelberg and Thornell (1983) have recently reported that some motor units from rat tibialis anterior muscle stained for Type I myosin ATPase, yet had the same contraction time as units from the soleus muscle that stained for Type II myosin ATPase. It was observed that the volume of terminal cisternae was equal in the two types of muscle fibres, despite their different myosin

ATPase staining characteristics. As they also found a high negative correlation between the contraction time of motor units and the volume of terminal cisternae in the corresponding muscle fibres, the authors suggested that the capacity of the terminal cisternae to release and then to take up Ca^{2+} is the primary factor in regulating the isometric twitch time course. However, it was also observed that in a given muscle, a larger volume of terminal cisternae was associated with fibres staining for Type II myosin ATPase. Thus, there was a relationship between type of myosin ATPase and twitch contraction time, but it was only applicable to fibres within the same muscle. These observations may explain why muscles with similar proportions of Type I and type II fibres may have different isometric twitch time-courses (Belanger et al., 1983).

The isometric twitch of aged muscle could be altered due to changes in one or more of the three factors discussed above. Little quantitative work has been done, however, to determine whether aging causes changes in the structure and function of the sarcoplasmic reticulum. Tomonaga (1977) and Shafiq et al. (1978) noted in a descriptive manner that t-tubule aggregations were occasionally observed in aged human muscle specimens examined under the electron microscope. As discussed earlier (see under heading, Muscle Histology), there are conflicting reports on whether muscles tend to lose Type II motor units preferentially. In relation to the stiffness of connective tissue, there are two reports that this is greater with aging, thus allowing for a more rapid transfer of tension developed by the muscle; nevertheless, twitches were longer in elderly than in young adults (Botelho et al., 1954; Campbell et al., 1973). These last

observations indicate that the other factors, muscle fibre type and/or regulation of intracellular Ca^{2+}, must have been more influential.

The amplitude of the isometric twitch is dependent not only on the amount of excitable muscle mass present, but also on the same factors which influence the twitch time course. Following a single excitation of the muscle the amount of time that the muscle actively generates tension will influence how much force is transmitted through the tendon. This is because the muscle must stretch the tendon before any tension is registered across the joint (Carlson and Wilkie, 1974). Furthermore, the stiffness of the tendon will also influence how much of the contractile force generated by a single excitation of the muscle is passed on. It has been observed that the twitch size was smaller in old muscles, despite a prolongation of the twitch duration (Campbell et al., 1973; Davies et al., 1983). Campbell et al. (1973) had also observed that the tendon was stiffer with aging and hence more effective in transmitting muscle tension. They concluded excitable muscle mass was considerably reduced in the elderly foot and this was indirectly confirmed by comparing the size of the compound muscle action potential between the young and old adults.

Innervation of Muscles

It is generally recognized that the motor neuron maintains the differentiated state of the muscle fibres which it innervates, so as to form a uniform motor unit (Buller et al., 1960; Edstrom and Kugelberg, 1968; Brandstater and Lambert, 1969). The strong possibility exists that with aging there is a disturbance of this "trophic" relationship,

resulting in the eventual loss of function in that particular motor unit (Campbell et al., 1973; McComas, 1977; Caccia et al., 1979). The way in which a nerve exerts its trophic action on muscle fibres is poorly understood but there is evidence that two mechanisms are involved: (1) impulse activity - the frequency or total number of excitations of muscle fibres (2) axoplasmic flow of messenger substances that are manufactured in the nerve cell body and transported along its axon, before crossing the neuromuscular junction into the muscle fibre (see Guth, 1968 and Pette, 1980 for reviews). It is possible that with aging decreases occur in both impulse activity and axoplasmic transport (Gutmann and Hanzlikova, 1972; Sprott and Eleftheriou, 1974; Stromska and Ochs, 1982).

There is evidence that the numbers of motor neurons are decreased in elderly humans. Gardner (1940) counted the number of myelinated fibres in the eighth and ninth thoracic ventral roots of cadavers between the ages of 34 and 85. When these data were combined with those from an earlier study (Corbin and Gardner, 1937), a 25% to 30% decrease in nerve fibre numbers was estimated to have occurred between the third and eighth to ninth decades. However, the cases were diseased, which makes for difficulty in assessing how much the aging influence alone was responsible for their findings.

Tomlinson and Irving (1977), in their study of aging and lumbrosacral motor neuron cell body counts, selected only those autopsy cases in which people had been healthy and died rapidly "from states of activity considered normal for the age." Their data seemed to show no changes in cell body numbers through the adult years until the seventh decade; then between the seventh and tenth decade, there was about a

30% to 35% decrease. Both alpha and gamma motor neurons were included in their cord sections; the latter type of cells innervate intrafusal fibres of the muscle spindle rather than extrafusal skeletal muscle fibres and it is not clear how they are affected by aging (Tomlinson and Irving, 1977).

McComas and co-workers sought to estimate the number of functioning motor units in living, healthy elderly people using a non-invasive electrophysiological technique (Campbell et al., 1973). With this method, the average size of an individual motor unit potential was estimated and then divided into the compound muscle action potential to obtain motor unit counts. Individuals of varying ages were tested for counts in the extensor digitorum brevis muscle of the foot, and the thenar and hypothenar muscles of the hand (Campbell et al., 1973; Sica et al., 1974; McComas, 1977). In each muscle motor unit counts were similar in adults up to age sixty but then were decreased by at least 50% in older people in their seventh decade. Other investigators have supported this finding of a decrease in motor unit counts with aging (Brown, 1973; Hansen and Ballantyne, 1978; Stalberg and Fawcett, 1982).

Motor unit counts seemed to be considerably lower than expected from other aging studies of motor neuron number or of muscle strength. However, McComas (1977) has postulated that some motor neurons present in the aged individual are no longer functional. In addition, through the process of collateral reinnervation surviving motor neurons may capture muscle fibres which have lost their original innervation; hence neurons are lost but not muscle tissue. In accordance with this reinnervation process, motor unit potentials were larger in the

elderly, which reflected an expanded motor unit size (Brown, 1973; Campbell et al., 1973; Hansen and Ballantyne, 1978; Stalberg and Fawcett, 1982).

Unfortunately, motor unit counting has been limited to small distal muscles which may be particularly susceptible to aging effects. The long axon required to innervate a distal limb muscle motor unit may be especially prone to degenerative changes with aging (Cavanagh, 1964; Campbell et al., 1973; Sabin, 1982), thereby leading to excessive motor unit losses. However, proximal muscles are not suitable for motor unit counting, because of their sizes, complex innervation patterns and inaccessible motor nerves.

Aging Studies in Animals

Changes in muscle structure with aging. Analysis of neuromuscular systems from young and old animals of the same strain has permitted quantification of aging effects on muscle morphology, histology and innervation. Most of the studies have been performed on rats or mice, and decreased numbers of fibres in rodent limb muscles have been consistently observed in older animals (Rowe, 1969; Tauchi et al., 1971; Gutmann and Hanzlikova, 1972; Hooper, 1981). This decrease in fibre number may be partially offset by fibre hypertrophy with aging (Rowe, 1969; Hooper, 1981). Another finding of Hooper (1981) was that fibre length was less in the biceps brachii and tibialis anterior muscles of old mice due to a loss of sarcomeres, but no change was observed in the average sarcomere length. The actual limb lengths were not reported.

It has been of particular interest to know whether the two functionally different muscle types, phasically and tonically active, vary in their susceptibility to aging effects. Tucek and Gutmann (1973) observed in rats that the decline in fibre number was greater in the predominantly Type I (tonic) soleus muscle as compared to the Type II (phasic) extensor digitorum longus (EDL). In rat EDL muscle there is an overall increase in the proportion of Type I muscle fibres (Caccia et al., 1979), yet in the rat tibialis anterior, Tauchi et al. (1971) reported a striking decrease in the proportion of "red" (tonic) muscle fibres. In the young rat, the tibialis anterior had approximately equal proportions of the two muscle fibre types; but with aging "white" fibres predominated.

For the mouse, Banker et al. (1983) have reported that the soleus muscle fibres were significantly smaller in older animals, but EDL fibres did not show any decrease. On the other hand, Rowe (1969) observed a trend to increased soleus fibre size in their old mice, although the mean age of the animals was 25 months, versus ages of 28 to 33 months in Banker et al.'s (1983) study.

Gutmann (1977) has proposed that rat motor units undergo a process of "de-differentiation" with aging, in which some of their specialized properties are lost. For example, highly differentiated muscles, such as soleus and extensor digitorum longus, become more similar in very old age (Gutmann and Syrovy, 1974; Caccia et al., 1979). In the adult rat the soleus muscle appears to first go through a stage of additional prolongation of the twitch concraction time (Vyskocil and Gutmann, 1972; Gutmann and Syrovy, 1974), and an enhancement of Type I myosin ATPase activity (Syrovy and Gutmann, 1970; Caccia et al., 1979), before

this final de-differentiation.

A common generalization about old muscles, both animal and human, is that there is an increase of fat and connective tissue to replace lost or atrophied muscle fibres (Lowry et al., 1942; Verzar, 1959; Jennekins et al., 1971; Borkan et al., 1983; Ludastcher et al., 1983), yet this has not been accurately quantified. In some muscles of the mouse there does not appear to be an increase in non-contractile tissue however, because muscle weight changes can be accounted for entirely by the decrease in fibre number (Hooper, 1981). Discrepancies could exist between different species and also because animals of various ages have been used in studies of "aging" rodent muscle. For example, Gutmann et al., 1971 used three month old, immature animals as controls; in other studies (e.g. Tauchi et al., 1971; Hooper, 1981) the aged animals were actually middle-aged and very old animals were not included. It is important to choose a healthy strain of mice or rats in which the growth pattern and life span has been clearly documented.

Characteristics of the aging neuromuscular junction. Effects of aging on the function of the neuromuscular junction (NMJ) have much bearing on the maintenance of normal muscle properties. In a comprehensive study of the effect of aging on the ultrastructure and physiology of mouse NMJs, Robbins and co-workers have compared the tonic soleus and phasic EDL muscles (Fahim and Robbins, 1982; Banker et al., 1983; Kelly and Robbins, 1983). Presynaptic ultrastructural changes included decreases in nerve terminal area, mitochondria and synaptic vesicles and increases in smooth endoplasmic reticulum, coated vesicles, cisternae, microtubules and structures identified as

neurofilaments. Post-synaptic differences in old NMJs included increases in the complexity of junctional folds, and also increases in subsarcolemmal vesicles and lipofuscin deposits (Fahim and Robbins, 1982). These changes were thought to be signs of "an age-related form of remodelling and morphologic adaptation." Aging changes were observed more frequently in the soleus than EDL muscle, but significant differences varying from 11% to 135% were found in both muscles when the numbers or sizes of various NMJ structures were compared in young and old animals.

Fahim and Robbins (1982) found few areas of complete denervation, but most of the old muscle fibres examined had post-synaptic changes. Caccia et al. (1979) proposed that denervation of muscle fibres in their old mice had occurred, but then the fibres had been reinnervated by the surviving motor neurons. Evidence for this process was their observations that the numbers of motor axons and motor units was reduced, but not the sizes of the compound muscle action potential or twitch tension. Fahim and Robbins (1982) criticized this work because immature 2-3 month old mice had been used as controls.

In the aged rat, Gutmann and co-workers did not find any decrease in motor neuron numbers, nor evidence of denervation, at a time when muscle atrophy and disorganization was present (Gutmann and Hanzlikova, 1966; Gutmann et al., 1971). However, Fujisawa (1976) observed deterioration in the distal portion of old rat motor neurons and Caccia et al. (1979) reported a decrease in the number of rat soleus motor units with aging. At least part of the explanation for these discrepancies lies in the use of different animal models and strains by the various investigators. As Fahim and Robbins (1982) have noted, the

commonly used laboratory rat may be a poor model for studies of pure aging effects because it becomes inactive, obese and has organ pathology in late life. An additional consideration is that some of the old nerve axons observed under the microscope in anatomical studies may have become non-functional.

A detailed examination of neuromuscular transmission has been undertaken by Robbins and co-investigators in several muscles of the CBF-1 mouse; this strain maintains its activity and freedom from organ pathology into advanced age. Miniature end-plate potentials (m.e.p.p.s.), caused by the spontaneous release of single acetylcholine (Ach) vesicles, were of similar amplitude in young and old soleus and EDL preparations, despite an increase in the input resistance of aged muscle fibres. Another finding was that the frequency of m.e.p.p.s. observed was decreased with aging (Banker et al., 1983). As the evoked end-plate potentials, recorded when the motor neuron was stimulated, were markedly increased in the older animals, it was concluded that the number of Ach vesicles released upon nerve stimulation was significantly greater with aging (e.g. estimated quantal content was increased about 2 to 3 times in older NMJs, depending on the method used for determining the number of Ach vesicles released, see also Kelly and Robbins, 1983).

Banker et al. (1983) found that the threshold level of depolarization required for initiation of the muscle action potential was unchanged in the old mouse preparations but end-plate potentials were increased; thus, the relative safety factor for excitation (synaptic efficacy) was enhanced in old NMJs. This increase in efficacy was also demonstrated by the observation that old NMJs were

less affected when the calcium/magnesium ratio in the bathing solution was lowered (this procedure hampers Ach release). In another study, Kelly and Robbins (1983) have shown that the enhancement of synaptic function took place in middle age for this strain and that the EDL muscle was affected at an earlier age than the soleus. Another observation was that the diaphragm showed less change with aging than the soleus muscle. Vyskocil and Gutmann (1972) have also noted in the rat that the frequency of m.e.p.p.s. recorded was much more reduced in the soleus muscles of old rats than in their diaphragms.

The functional consequences of these aging changes at the NMJ are two-fold. First, the reduction in m.e.p.p. frequency was indicative of a diminished rate of spontaneous acetylcholine release . However, the likelihood of excitation of a muscle fibre by the initial impulses of its motor neuron was increased due to the enhanced Ach release and hence end-plate potential size. Kelly and Robbins (1983) considered this enhancement of neuromuscular transmission to be a compensatory response, although it should be noted that during prolonged signalling the aged synapse might be less able to prevent exhaustion of Ach vesicles. The stimulus for this adaptation remains undetermined, but it was observed that the changes were present in middle-aged rats, at a time when there was no evidence of other pathology. One possibility is that changes at the NMJ are part of a normal developmental/maturation/aging sequence that takes place independently of changes in activity pattern or disease.

Summary of Literature Review

Strength in maximum voluntary muscle contractions (MVC) is less in old-adults than young men and women. Most investigations have indicated that isometric MVC is relatively constant through middle age and marked decreases take place in the sixth and seventh decades. Muscles acting at the ankle, knee, hand and elbow appear to show the same general pattern of change in the elderly. Extraneous variables such as size and activity pattern have not always been controlled for in these cross-sectional studies, but results from a longitudinal study were consistent with the rest. Opposing muscles at a joint have been compared in only one study of men. There have been few studies on women and very old individuals of either sex have seldom been included in aging studies to date.

A loss of excitable muscle mass is the likely explanation for declines in MVC with aging, although a lack of motivation for tests and/or a lack of nervous coordination have not been evaluated. McComas and co-workers have reported that the healthy elderly have a decreased number of motor units in the small distal muscles of the hand and foot. Although initially over-sized motor units, due to a collateral re-innervation process, may compensate for the denervating process, a loss of muscle fibres seems to be inevitable. Atrophy of muscle fibres does not seem to be a general feature of aging. Controversy exists on whether the proportion of Type II and Type I muscle fibres changes with aging, but it has been clearly demonstrated that the isometric muscle twitch is prolonged. Other factors influencing twitch times, such as the regulation of free calcium ions in the muscle sarcoplasm by the

sarcoplasmic reticulum, and tendon properties, could also change with aging.

Observations on the effects of aging in animal tissue have shown that muscle fibre loss occurs without generalized muscle fibre atrophy. There is no consistent trend to demonstrate greater aging effects on tonically active or phasically active muscles. Controversy exists over whether old rodent muscles undergo a denervation process. Robbins and co-workers have presented evidence that adaptations at the mouse neuromuscular junction take place in middle-age and increase the likelihood of successful synaptic transmission. The stimulus for such adaptations could arise as part of a normal developmental/maturation/aging progression, which is independent of changes in activity pattern or disease.

II. METHODS

A. Subjects

The subjects were 116 Caucasian men and women whose ages ranged from 20 to 100 years. They were divided into 5 groups on the basis of age; each group corresponding to approximately one decade (20-32, 40-52, 60-69, 70-79 and 80+ yr; see Table 2). Volunteers were recruited by advertising in the McMaster University and Hamilton media; they came from all parts of the Hamilton area. The older subjects were still living independently in the community; most still maintained their own homes and the rest came from other settings such as senior citizen apartments.

The elderly subjects reported they were in good health at the time of the test. All were mentally competent and cooperative with the test procedures. Everyone could walk independently, without aids, and most stated that daily walking was a part of their normal activity. Some of the subjects in their 60's and 70's also engaged in more strenuous activity patterns such as jogging, swimming and sports/fitness programs at local exercise facilities. Other evidence of the healthy state of these subjects was that very few reported taking daily medication (a small number were on anti-hypertensive drugs). Volunteers were not considered for testing if they had diseases known to influence peripheral nerve and muscle function such as diabetes, thyroid disorders, arthritis, or activity-limiting cardiovascular disease. A year after testing most of the study participants responded positively

Table 2. Subject Characteristics by Age and Sex Groups

	Sex		Age Group (Yr) 20–32	40–52	60–69	70–79	80–100
Number	M		14	10	13	16	13
	F		13	10	10	9	8
Age (Yr)	M	$\bar{x}$	27.4	43.7	65.3	74.0	87.2
		SD	2.7	2.7	3.7	2.5	6.9
	F	$\bar{x}$	27.0	44.0	64.9	74.2	88.6
		SD	3.7	4.0	2.9	3.5	7.2
Height (cm)	M	$\bar{x}$	176.7	176.8	172.4	174.7	167.4
		SD	6.9	5.9	5.6	9.4	3.7
		Range	165–186	167–184	164–180	158–194	162–175
	F	$\bar{x}$	160.2	162.9	159.7	162.4	155.4
		SD	5.7	6.5	7.6	5.5	6.1
		Range	148–170	155–174	151–173	156–170	144–164
Weight (kg)	M	$\bar{x}$	72.3	77.5	73.8	71.5	66.8
		SD	8.2	12.4	12.0	9.3	5.9
		Range	56.0–82.2	59.4–99.9	57.6–94.7	60.1–94.0	57.8–78.2
	F	$\bar{x}$	54.4	66.0	60.5	58.8	53.5
		SD	6.0	10.3	7.8	9.9	8.2
		Range	45.0–67.0	46.8–79.5	50.6–75.6	38.9–68.8	42.4–63.8

to a request for their involvement in another, unrelated research project. It was thus learned in this indirect manner that survival rate was very high in the elderly subjects for the year after investigation.

Healthy younger subjects were selected on the basis of their having comparable activity patterns to the old adults. None of the young adults were engaging in strenuous endurance training or in a "resistance" type of training that would lead to muscle hypertrophy. Younger subjects' occupations were sedentary, involving sitting at a desk for most of the time with some standing and walking. Subjects of various sizes were chosen for the study, excepting obese individuals (see Table 2).

B. Experimental Procedures

I. Subject Orientation. The test began with an orientation of subjects to (1) the purpose of the study, (2) the procedures of the test, and (3) any risks or discomfort involved. They were assured of their confidentiality in the research program and asked to sign a written consent form (see Appendix 1). Subjects were then questioned about their health history, including daily activities, and height and body weight were measured.

II. Apparatus for Measuring Tension Produced at the Ankle Joint. Subjects were fitted in the leg-holding apparatus pictured in Fig. 1. They sat on a modified chair in which the seat could be raised or lowered according to the subject's leg length. Normally, the right foot was fixed in place on the padded foot-plate of the leg-holding

Figure 1. Apparatus for measuring neuromuscular function at the ankle joint. Note the fixation of the foot and leg in the isometric test position. The subject, a 100 year old man, was observing his voluntary torque output.

device by securing velcro straps over the top of the foot. A clamp over the knee was used to prevent raising of the heel. The knee joint angle was set at 90° by adjusting the height of the chair seat. Subjects were made as comfortable and as stable as possible in the chair; this stability ensured that they could relax their muscles completely. Finally, the leg was warmed by a heat lamp to maintain lower leg skin temperature at 34 to 37°C.

Both passive tension about the ankle joint and muscle contractile properties were measured by registering the torque produced on the steel foot-plate. The horizontal axis of rotation of the foot-plate coincided with the axis through the subject's ankle joint. The plane of the foot-plate could be set at up to 40° from the horizontal in either direction. Pressure from torques acting on the foot-plate was sensed by strain gauges mounted on a rigid bar, this bar being attached perpendicularly to the foot-plate (see Fig. 2). The electrical signal from the strain gauges was preamplified before being passed to a variable-persistence cathode ray storage oscilloscope (Hewlett-Packard type 141B); the frequency response of the device was 85 Hz. Calibration of the system with known torques of up to 250 N.m (Newton metres) demonstrated that it was accurate for the range of torques measured in this study and that distortion of the foot-plate was minimal.

III. Main Test Protocol. A total of 111 subjects, 63 men and 48 women, participated in the procedures of the main test protocol, which are outlined in Table 3 and detailed below:

(i) Passive tension. Preliminary experiments were done to determine

Figure 2. The rotatable foot-plate. Strain gauges attached to the metal tongue underneath the foot-plate recorded torques generated about the ankle joint. Joint position could be varied 40^{o} from the horizontal plane in either direction.

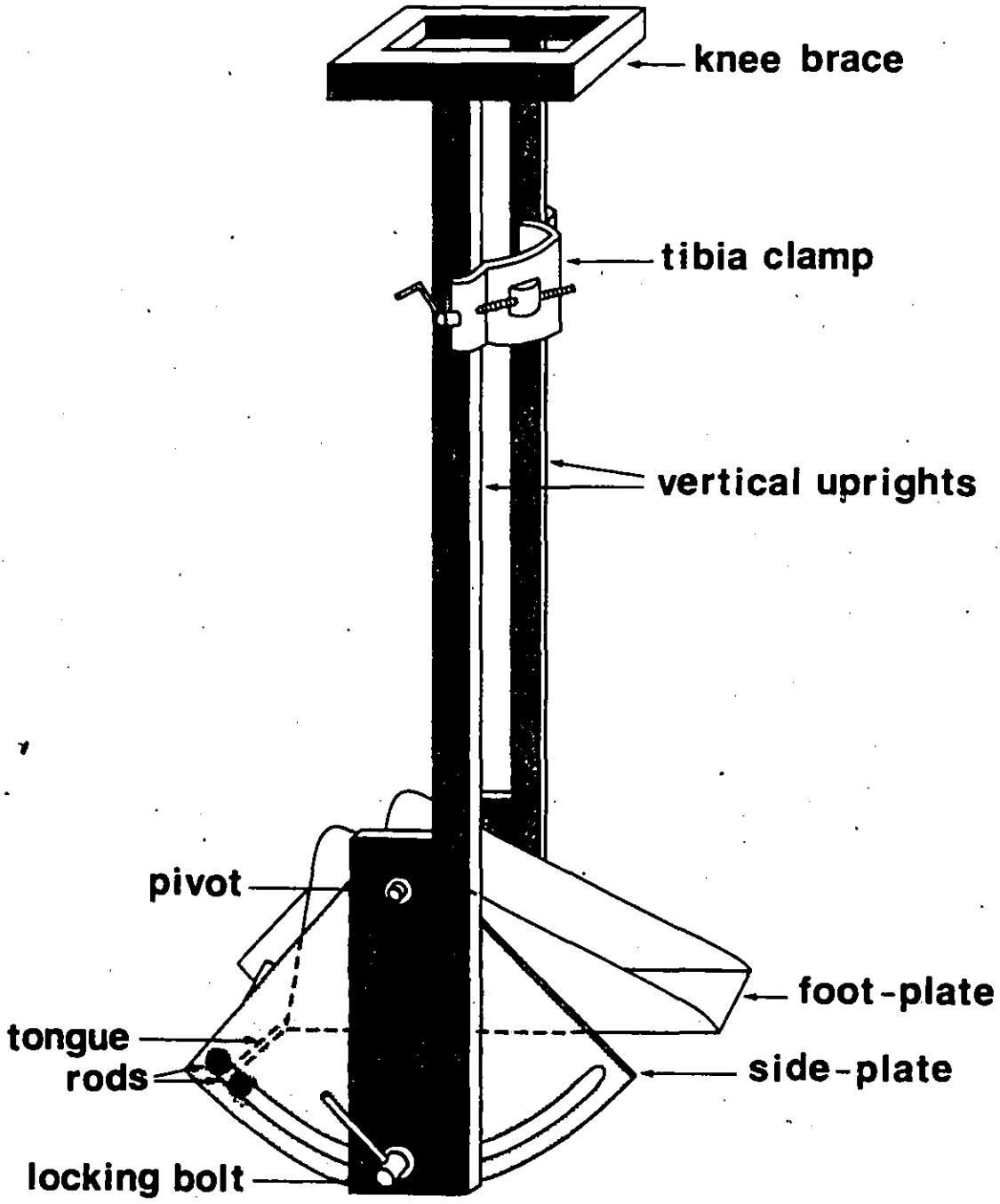

knee brace
tibia clamp
vertical uprights
pivot
foot-plate
tongue
rods
side-plate
locking bolt

Table 3. List of Experimental Procedures.

1. Subject Orientation

2. Main Test Protocol
   - (i) Passive tension
   - (ii) Passive range of ankle joint movement
   - (iii) Resting isometric twitch properties of the dorsiflexor muscle group
   - (iv) Potentiated isometric dorsiflexor twitch properties
   - (v) Isometric dorsiflexor maximum voluntary contraction, including assessment of the extent of motor unit activation by using the interpolated twitch procedure
   - (vi) Resting isometric twitch properties of the plantarflexor muscle group
   - (vii) Potentiated isometric plantarflexor twitch properties
   - (viii) Isometric plantarflexor maximum voluntary contraction, including assessment of the extent of motor unit activation by using the interpolated twitch procedure

3. Sub-protocol for Assessing Reliability of Measures

4. Sub-protocol for Measuring Twitch Times in the Lateral Gastrocnemius, Medial Gastrocnemius, and Soleus Muscles Individually

5. Sub-protocol for Measuring Cross-sectional Areas of the Gastrocnemius and Soleus Muscles

that the average resting position of the ankle joint in the foot-holder was at 10^{o} of plantarflexion (that is, 10^{o} of downward rotation of the foot-plate from the horizontal). Thus, passive tension was measured as the torques created about the ankle joint by stretches from 10^{o} to 20^{o},30^{o} and 40^{o} of plantarflexion (P), and from 10^{o}P to 0^{o},10^{o} and 20^{o} of dorsiflexion (D). The foot-plate was fixed in these positions in a random order. Readings were taken only after the subject had relaxed his or her muscles completely, as determined by a silent electromyographical (EMG) signal (see description of EMG recording in Part iii below). Passive tension values were reported for the two test positions used during isometric strength and twitch measurements, namely, 10^{o}D and 30^{o}P (test positions for the plantarflexor and dorsiflexor muscles respectively). Correction was made for the gravitational torque created by the weight of the foot and foot-plate at these positions.

(ii) Passive range of ankle joint movement. Ankle joint flexibility was assessed by measuring the extent to which the ankle could be dorsiflexed with the subject's foot placed in the foot-holder (due to the design of the foot-holder, the limit of plantarflexion could not be assessed in the same way). The value recorded was the highest degrees of dorsiflexion reached during 3 attempts to rotate the foot-plate upwards as far as possible from the neutral position (sole of foot perpendicular to tibia).

(iii) Resting isometric twitch properties of the dorsiflexor muscle group. A position of 30^{o}P was used to test the dorsiflexor muscle group in this part of the protocol. This position was chosen because the dorsiflexor group was stretched to an optimum length for

active tension development. Furthermore, confounding effects arising from activity of the antagonistic plantarflexor muscles were minimized when the ankle was placed in this position. Elimination of the effects of antagonistic muscles was particularly important during electrical stimulation of the leg (Marsh et al., 1981; Sale et al., 1982). Stimulating electrodes for evoking twitches were two strips of aluminum foil, approximately 3X5 cm in size, connected to a Devices Ltd constant voltage stimulator (Type 3072). The cathode was attached to the skin overlying the common peroneal nerve near the head of the fibula; the anode was situated on the uppermost part of the tibialis anterior muscle. This electrode arrangement was chosen over others because it required lower stimulus voltages and was less likely to activate the tibial nerve. Although the anode was distal to the cathode, the stimulating pulses were too brief (50-100 us) for anodal block to interfere with impulse propagation from the cathode to tibialis anterior.

For these and all other electrodes, the skin was prepared by cleansing with rubbing alcohol; electrode-skin contact was further facilitated by application of standard electrode gel. Single pulses of current, lasting 50 or 100 microseconds, were triggered from a Devices Ltd digitimer (Type 3290). The stimulus intensity was gradually raised to a level supramaximal to that required for maximal twitch tension; this level ensured that muscle excitation remained complete throughout the test. The effective impedance of the stimulating electrodes varied from subject to subject, but ordinarily, the maximum stimulator intensity setting was between 200 and 300 volts.

When a maximal twitch had been obtained, recordings were made of:

(1) the peak-to-peak amplitude of the compound muscle action potential (M-wave), (2) the twitch contraction time (CT), (3) the one-half relaxation time (1/2 RT) and (4) the peak level of the twitch torque (peak twitch torque, P_t). The respective measurement procedures are illustrated in Fig. 3. M-waves were led off from the dorsiflexor muscle group by placing a stigmatic recording electrode on the skin over the belly of tibialis anterior. A reference electrode was attached over the distal tendon of tibialis anterior. The recording electrodes were Beckman silver cups with 7 mm diameters. A silver strip ground electrode was placed between the stimulating anode and the stigmatic recording electrode (see Fig. 4). The EMG signal was preamplified before being sent to the variable-persistence storage oscilloscope for measurement.

Twitch times were measured on a digital analyzer (Hewlett-Packard Type 5480B). The torque-time signal of the twitch was differentiated by an electronic circuit to facilitate accurate identification of the onset of the twitch and the moment when it reached its maximum torque; peak twitch torque was measured on the variable-persistance storage oscilloscope. Subjects were taught to relax their muscles by listening to a loudspeaker connected to the EMG amplifier. If the muscles had been active, adequate rest was allowed before stimulating, because even brief activity has been shown to have effects on the twitch response (Vandervoort et al., 1983).

(iv) Potentiated isometric dorsiflexor twitch properties. Subjects were instructed to make isometric maximal voluntary contractions (MVCs) of their dorsiflexor muscles for 5 seconds, in response to a timer light mounted in front of them. Several practice attempts were taken

Figure 3. Analysis of the isometric muscle twitch. M-wave = compound muscle action potential, CT = twitch contraction time, 1/2 RT = one-half relaxation time and P_t = peak level of the twitch torque. See text.

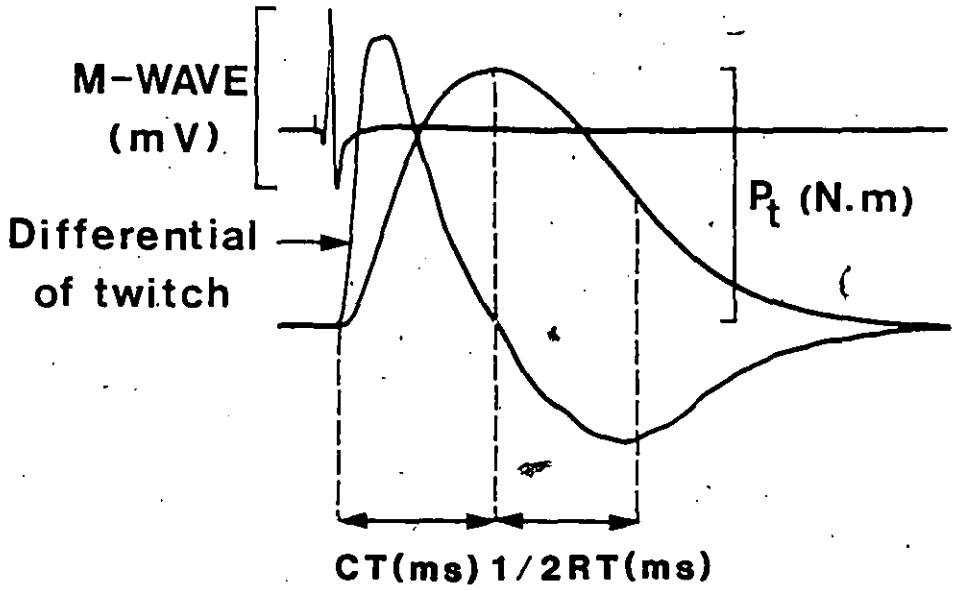
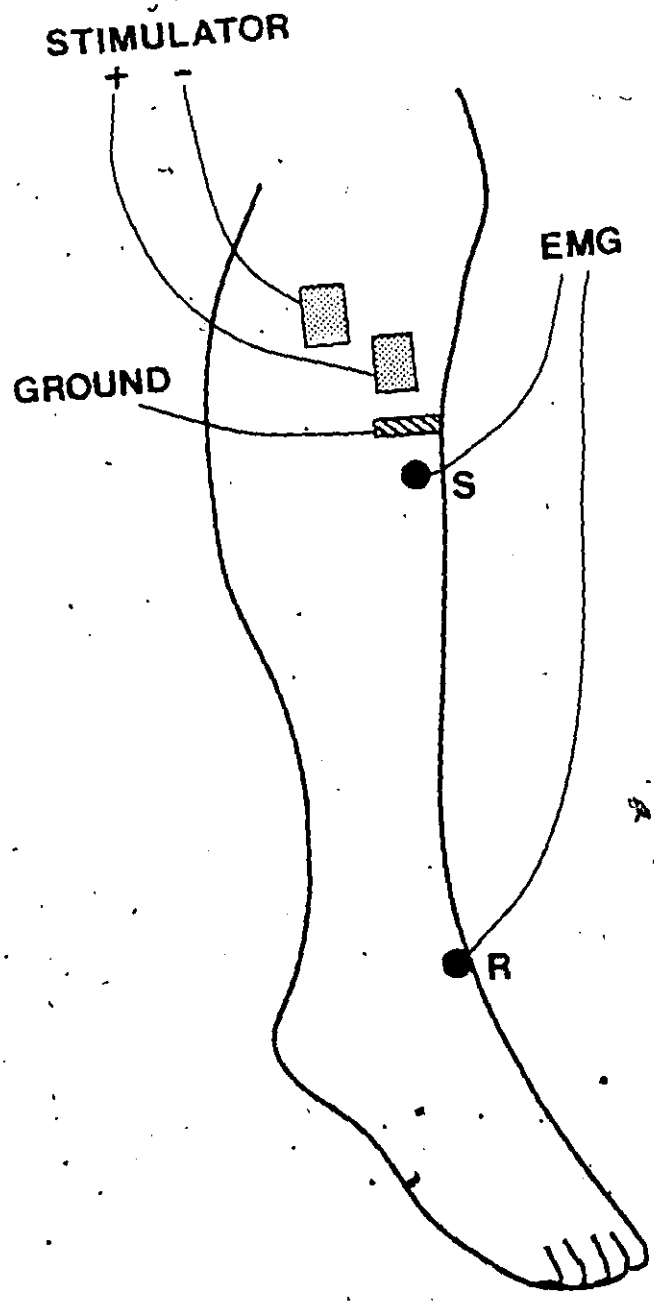

M-WAVE
(mV)
Differential
of twitch
P_t (N.m)
CT(ms) 1/2RT(ms)

Figure 4. Location of the stimulating and recording electrodes on the dorsiflexor muscle group. See text.

S: stigmatic electrode

R: reference electrode

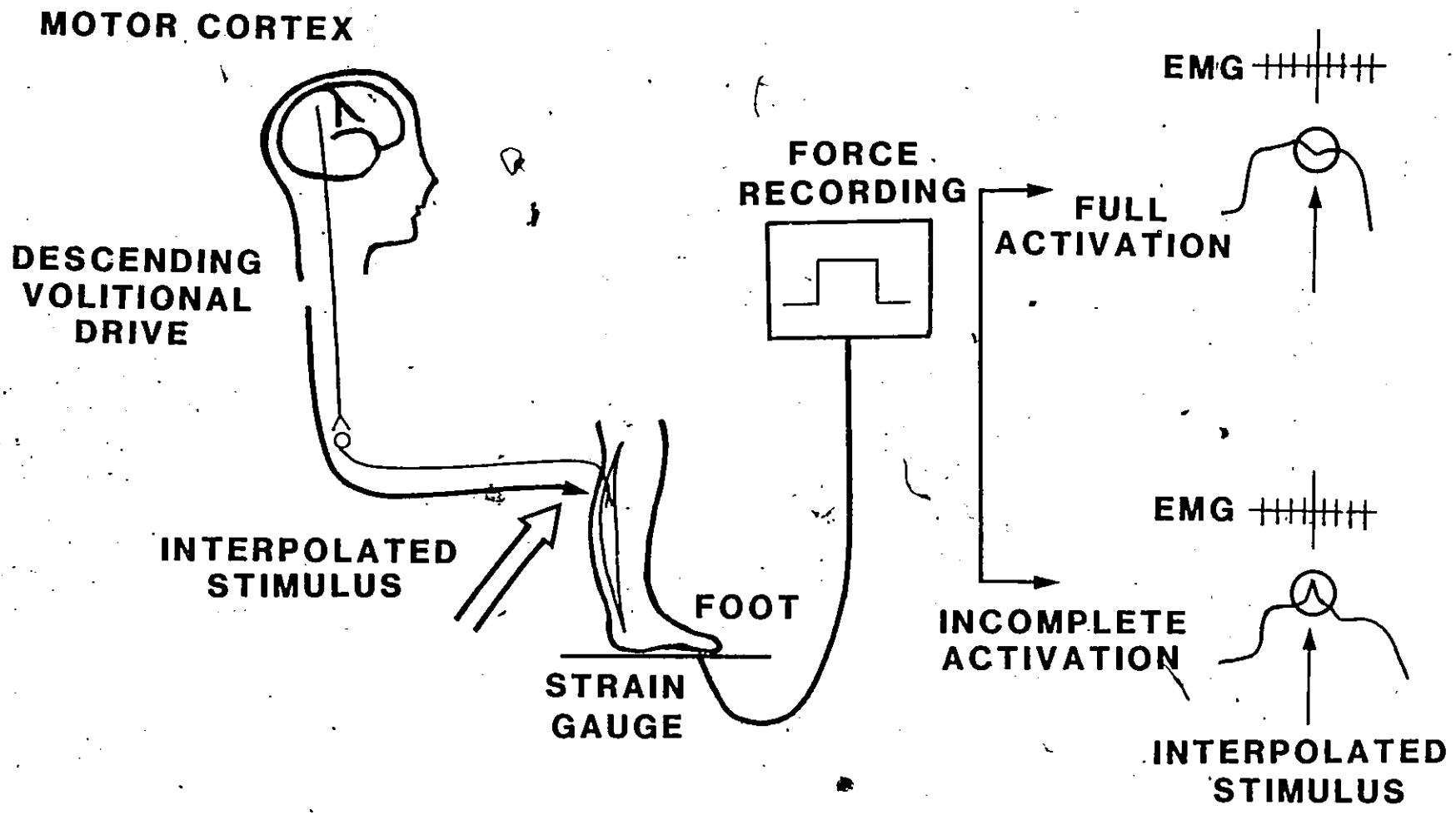
(Diagram from Fitch, 1983)


STIMULATOR
+
-
EMG
GROUND
S
R

to familiarize subjects with the task. They then made a 5s MVC, relaxed immediately afterwards, and received a twitch stimulus. This stimulus, timed to elicit a twitch 3s post-exercise, was of the same strength as that for the resting twitch. M-wave, contraction time, one-half relaxation time and peak twitch torque values were recorded for the potentiated twitch.

(v) Isometric dorsiflexor maximum voluntary contraction. Subjects were given several attempts to achieve as high a torque recording as possible during voluntary contraction of the dorsiflexors. MVCs were 5s in duration and were timed by a light as in the potentiated twitch procedure. During MVCs, a single twitch stimulus was applied to assess whether the subject was able to activate his or her muscles optimally for maximum dorsiflexor tension development (see Fig. 5). If a subject had achieved full motor unit activation, then the stimulus produced no increase in the torque output. This technique of twitch interpolation during MVC was modified slightly from that used by Belanger and McComas (1981); in the present investigation the entire dorsiflexor muscle group was stimulated, rather than just the tibialis anterior muscle. The technique proved useful as a means for motivating subjects if incomplete muscle activation was present. Additional forms of encouragement for the subject to exert as strong an effort as possible were: (1) the biofeedback obtained from the EMG signal directed through a loud-speaker, (2) the visual feedback of the torque record on the oscilloscope, and (3) the examiner's verbal support. Attempts at MVC were continued until either no interpolated twitch was present or, in the case of incomplete muscle activation, the torque output became constant after several additional trials. Adequate rest was allowed

Figure 5. Use of the interpolated stimulus technique to assess completeness of motor unit activation during MVC. The stimulus did not increase the torque record if full voluntary activation was present.


MOTOR CORTEX
DESCENDING VOLITIONAL DRIVE
INTERPOLATED STIMULUS
FOOT
STRAIN GAUGE
FORCE RECORDING
EMG
FULL ACTIVATION
EMG
INCOMPLETE ACTIVATION
INTERPOLATED STIMULUS

between trials. The highest torque achieved was reported as the subject's maximum voluntary strength.

(vi) Resting isometric twitch properties of the plantarflexor muscle group. Initially, the back of the lower leg was heated until skin temperature over the plantarflexor muscle group reached 34-37°C. The foot-holder was placed at 10°D to optimize plantarflexor muscle tension generation and to minimize any confounding action of the antagonists during stimulation. Maximal twitches of the plantarflexor muscle group were evoked via an electrode-holder designed to fit snugly in the popliteal fossa. The cathode and anode were aluminum foil electrode surfaces, approximately 10 cm^2 in area. Procedures for skin preparation were similar to those used for the dorsiflexor muscle group. Maximal plantarflexor twitches were usually achieved with stimulus pulse durations of 50 or 100 microseconds, and with intensity settings of 260 to 400 volts. Stimulation intensity was made supramaximal to ensure complete muscle excitation throughout all test procedures.

The plantarflexor M-wave was recorded with silver cup electrodes like those used for the dorsiflexor group. The stigmatic electrode was placed over the soleus muscle, just below the point where the two gastrocnemii muscle bellies separate. A reference electrode was placed over the Achilles tendon and the ground was located on the tibialis anterior muscle. Isometric twitch properties were measured with the same methods as those used for the dorsiflexor muscle group.

(vii) Potentiated isometric plantarflexor twitch properties.

(viii) Isometric plantarflexor maximum voluntary contraction. The procedures for sections vii and viii were similar to those for the

dorsiflexor muscle group. First, subjects practiced voluntarily contracting the plantarflexor muscle group as strongly as possible. Belanger and McComas (1981) had demonstrated previously that the plantarflexor muscle group was more difficult to fully activate in a MVC than the dorsiflexor group. Therefore, the dorsiflexor group was examined first in all subjects, because this order of testing allowed familiarization with the apparatus before plantarflexor MVC trials were done. As reported in the Results section, all subjects achieved complete dorsiflexor activation during MVC, so this order of muscle testing was not detrimental to dorsiflexor MVC values.

IV. Sub-protocol for Assessing Reliability of Measures. On another day, measurements of passive tension, passive range of ankle joint movement, dorsiflexor MVC, plantarflexor resting and potentiated isometric twitch properties and plantarflexor MVC were repeated on 4 males, aged 69-85 yr, and 3 females, aged 62-82 yr (note: one woman did not complete the potentiation of plantarflexor twitch measurements). In addition, dorsiflexor and plantarflexor MVC were measured on 2 separate days for a 98 yr old woman and a 100 yr old man. See Appendix C.

V. Sub-protocol for Measuring Separate Twitch Times in the Lateral Gastrocnemius, Medial Gastrocnemius and Soleus Muscles Individually. Contraction times and one-half relaxation times were measured for the lateral gastrocnemius, medial gastrocnemius and soleus muscles of 8 older males, aged 69-100 yr, and 7 older females, aged 62-92 yr. In most cases this procedure was done in combination with the reliability sub-protocol. For a few subjects, however, this testing was done

during their first visit to the laboratory, in conjunction with the main test protocol. Similar twitch analyses of the lateral gastrocnemius, medial gastrocnemius and soleus muscles were performed for 6 young men and 6 young women. This was the only protocol in which 3 of these younger men and 2 of the younger women participated.

Twitches were elicited by stimulating the individual calf muscles submaximally via pairs of aluminum foil electrodes, 2X2 cm in dimension. Electrodes were placed over the respective muscle belly in a position where stimulation threshold was lowest. Other muscles were monitored by visual inspection and EMG recordings to ensure that stimulation was isolated to only the muscle under study. It was found that separate, measureable twitches of at least 0.5 N.m could be obtained with this method (Vandervoort and McComas, 1983); the maximal twitch of the entire plantarflexor group was also measured in this protocol. The order in which muscles were examined was randomized. The method of twitch time analysis has been described before in the sub-section on "Resting isometric twitch properties of the dorsiflexor muscle group".

(VI) Sub-protocol for Measuring Cross-sectional Areas of the Gastrocnemius and Soleus Muscles. Cross-sectional areas (CSAs) of the gastrocnemius and soleus muscles were obtained for 10 young (23-31 yr) and 10 very old (82- 100 yr) males and females (5 per age/sex group). Ultrasound films showing cross-sections of the lower leg were made with the use of the B-Scanner ultrasound imaging technique (Picker model). CSAs of the gastrocnemius and soleus muscles were then measured on a

computerized digitizing board (Numonics Clinical Analyzer) in a random, blind manner. The highest values from a series of films on each subject were reported. Five of the young adults (3 males, 2 females) had ultrasounds repeated on another day for the purpose of assessing measurement reliability.

C. DATA MANAGEMENT and STATISTICAL ANALYSIS

A complete set of data for the main testing protocol was obtained on 111 individuals. In a few instances data was missing, due to technical failures during the testing procedures or due to subject non-compliance (e.g., some subjects could not completely relax for passive tension measurements). In these cases, values were predicted from known relationships to other variables. Some of the subjects participated in additional sub-protocols after being selected for extreme age and/or willingness to return. An additional 5 young adults participated only in a pilot study on the individual contractile properties of the lateral gastrocnemius, medial gastrocnemius and soleus muscles (Vandervoort and McComas, 1983), and their data was included with that for other subjects tested in this sub-protocol.

Statistical analyses were done via BMDP computing packages (Biomedical programs, University of California, Los Angeles) stored on the HP3000 computer of the McMaster Medical Centre's Computational Services Unit. The data were examined with an analysis of variance to determine the effects of the two grouping factors, age group and sex. Group means and one standard deviation (SD) were calculated to allow for assessment of within-group variance and for the analysis of trends

in the data. In some cases data were normalized with respect to young adults' values to clarify change with age. Significant interactions between the two grouping variables were investigated further with the Newman-Keuls' multiple-range test of significance for differences between several means.

III. RESULTS

A. Relationship between Age and Voluntary Strength

Voluntary strength of the young and middle-aged adults was similar, but with advanced age clear decreases were observed (see Table 4; age group was a significant factor for both the dorsiflexor and plantarflexor muscles, ($p<.0001$). The mean values for strength of maximal voluntary contraction (MVC) of men and women in each age group are contrasted for the two muscle groups in Fig. 6; men were significantly stronger than women for both muscles ($p<.0001$ in each case). In both sexes the absolute decrease in MVC across age groups was much greater for the plantarflexor muscles than the dorsiflexor muscles (Table 4).

The influence of age on strength was compared between the two muscle groups in another way, by normalizing the data with respect to young adult values. The means of each age group of men and women are presented as percentages of the corresponding young adult value in Fig. 7. The normalized decreases in strength in the older age groups were generally the same for the dorsiflexor and plantarflexor muscles. Men and women in their seventh decade had mean strength values which ranged from 80% to 90% of those of young adults; in the 80 to 100 yr olds, the corresponding percentages were from 47% to 63%. Men showed larger decreases than women, with the exception of plantarflexor MVC in the oldest subjects.

As noted above, the general trend in the data was for MVC to decrease after middle-age (see Fig. 6). To illustrate this trend more

Table 4. Maximal Voluntary Strength of Males and Females in the Different Age Groups

Variable	Sex		Age Group (Yr) 20–32	40–52	60–69	70–79	80–100
N	M		11	10	13	16	13
	F		11	10	10	9	8
DF MVC (N.m)	M	$\bar{x}$	43.5	37.2	36.2	31.6	24.2
		SD	6.5	4.3	7.6	8.6	7.0
	F	$\bar{x}$	26.6	25.8	23.8	21.5	16.7
		SD	4.5	6.3	3.1	3.9	4.9
PF MVC (N.m)	M	$\bar{x}$	171.1	171.3	136.1	121.1	93.6
		SD	33.5	34.0	24.7	30.5	30.4
	F	$\bar{x}$	113.3	126.8	96.0	93.6	53.6
		SD	34.7	28.2	25.1	26.8	22.7

ANOVA Results

DF muscle:

Sex Effect, $F=93.93$, $df=1,101$, $p<.0001$

Age Group Effect, $F=16.43$, $df=4,101$, $p<.0001$

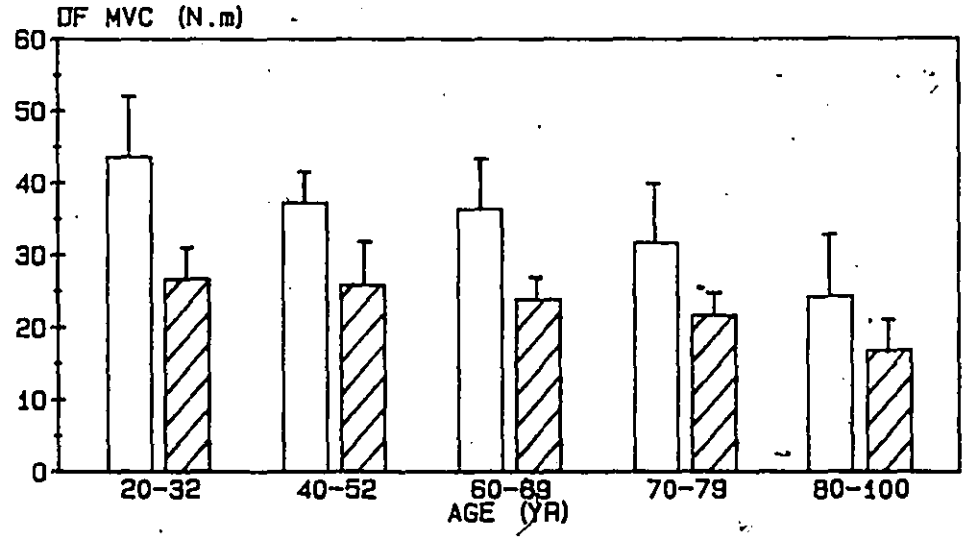
PF muscle:

Sex Effect, $F=54.09$, $df=1,101$, $p<.0001$

Age Group Effect, $F=21.14$, $df=4,101$, $p<.0001$

Interaction effects were not significant.

Figure 6. Maximal voluntary strength of the dorsiflexor (DF) and plantarflexor (PF) muscles in men and women aged 20 to 100 yr. Effects of sex and age group were significant in both muscle groups ($p<.0001$ for every variable). Means and 1 SD are shown; N=63M, 48F, range of 8 to 16 per group. Open bars = males.


DF MVC (N.m)
60
50
40
30
20
10
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

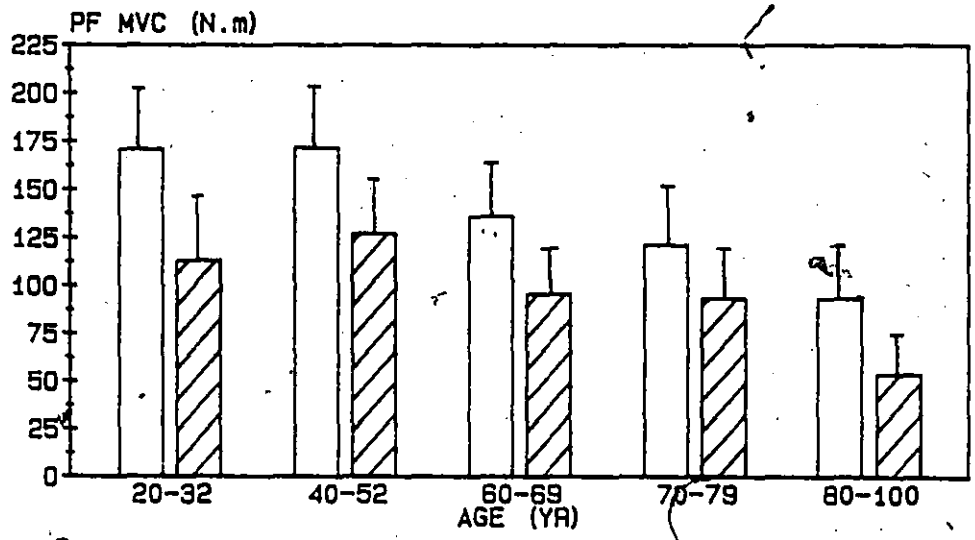
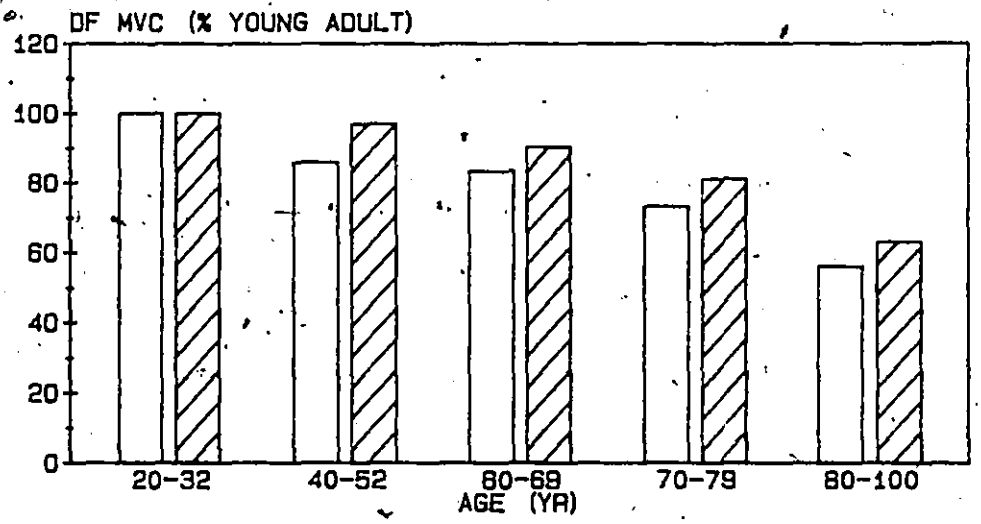
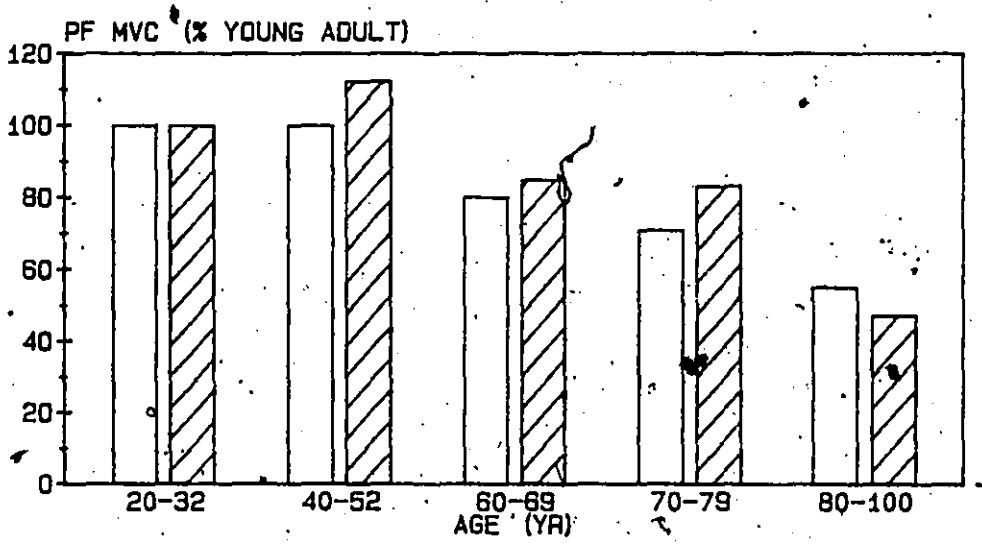

PF MVC (N.m)
225
200
175
150
125
100
75
50
25
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

Figure 7. Normalized mean MVC values. Percentages were derived from data of Fig. 6, by dividing into the appropriate male or female young adult mean. Open bars = males.


DF MVC (% YOUNG ADULT)
120
100
80
60
40
20
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

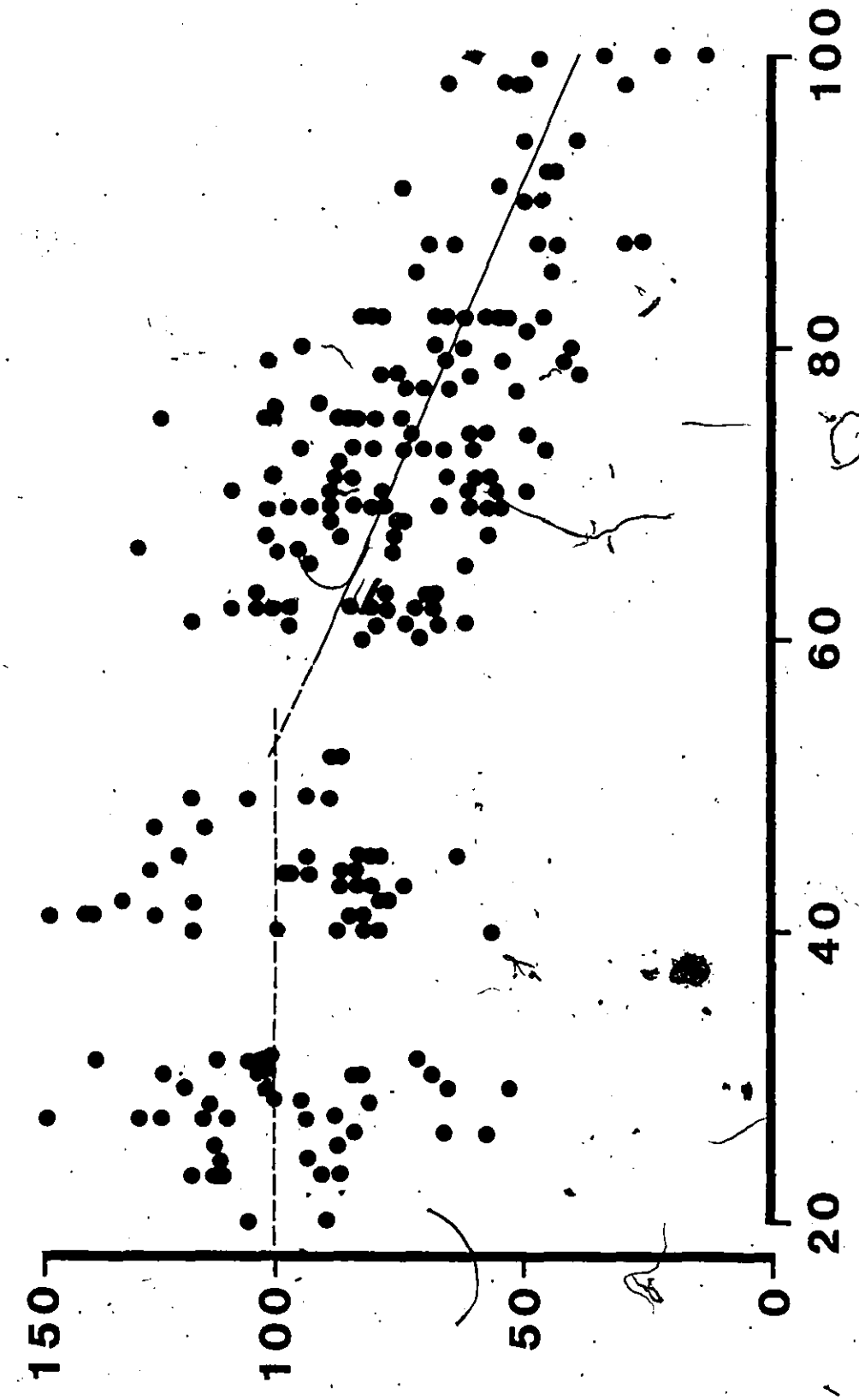

PF MVC (% YOUNG ADULT)
120
100
80
60
40
20
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

clearly, individual MVC values have all been normalized with respect to the appropriate young adult means and then plotted against age of the subject (Fig. 8). Inspection of the data suggested dividing the subjects into two groups for analysis, 20 to 52 yr olds, and those aged 60 to 100. There was in fact no relationship between normalized strength and age in the group of subjects between 20 and 52 yr, r= -0.043. In the 60 to 100 yr olds, the regression of strength on age was statistically significant; a linear correlation coefficient of -.604 was obtained ($p<.001$) and the regression line equation was: Normalized MVC = -1.295 (age in years) + 169.2. However, exceptional individuals were present in the 60 to 80 yr old age range whose values were equal to or greater than the average young adult.

Completeness of Motor Unit Activation during MVC

As described in the Methods section, an interpolated stimulus, delivered to the appropriate motor nerve, was used to test the completeness of motor unit activation during voluntary effort. All the young subjects (aged 20-32) proved capable of fully activating their dorsiflexor motor units and the same was true for the older adults. As regards the plantarflexor muscles, 3 of the 22 young adults could not completely activate their motor units, nor could 14 of the 63 subjects aged 60 yr or more. The proportions of such subjects did not differ significantly in the young and elderly groups. All of the middle-aged subjects achieved full activation of their plantarflexor motor units.

Figure 8. Individual normalized MVC values. Percentage values were derived by dividing each person's DF and PF maximal voluntary strength into the appropriate male or female young adult mean. N=111 subjects X 2 muscles. For the regression of normalized MVC on age in the 60 years and over group, $r = -.604$ ($p < .001$) and the equation was $Y = -1.295 (X) + 169.2$, N = 138 points. For results in subjects aged 52 or less, $r = -.043$, N= 84 points.


NORMALIZED MVC$_s$
(% YOUNG ADULT MEAN)
150
100
50
0
20
40
60
80
100
AGE (YEARS)

B. Cross-sectional Areas of the Plantarflexor Muscles in Young and Old Adults

The striking loss of plantarflexor muscle strength was investigated further by measuring cross-sectional areas of the gastrocnemius and soleus muscles in young and old adults. As shown in Table 5, the effect of aging was similar on the two muscles, hence the data was pooled for further analysis. The combined cross-sectional area of the gastrocnemius and soleus muscles was significantly greater in males than females ($p<.005$, see Table 5). Old men (aged 85 to 100 yr) and old women (aged 82 to 98 yr) had significantly smaller cross-sectional areas than their young adult counterparts ($p<.001$). An example of an ultrasound comparison of the legs of a young and an old man can be seen in Fig. 9. Orientation to landmarks created by the highly reflective interfaces between different types of tissue (e.g. muscle/connective tissue) allowed for tracing of muscle outlines with acceptable reliability of measurement (see Appendix C).

The difference in plantarflexor strength between young and old adults was greater than that for plantarflexor cross-sectional areas (note Fig. 9). Hence, the strength per cross-sectional area of muscle was significantly less in the old ($p<.01$, Table 5). These ratios did not differ significantly between the sexes (see Fig. 10).

Table 5. Cross-sectional Area (CSA) of the Gastrocnemius and Soleus Muscles and Ratio of PF MVC to CSA in Young and Old Adults

Variable		Young Adults M	Young Adults F	Old Adults M	Old Adults F
CSA (cm^2)					
Gastroc.	$\bar{x}$	17.7	15.6	13.2	9.7
	SD	2.8	1.6	2.5	2.4
Soleus	$\bar{x}$	18.8	15.7	14.8	11.1
	SD	3.0	2.0	2.8	1.6
Combined	$\bar{x}$	36.5	31.3	28.0	20.9
	SD	5.3	2.0	5.1	3.8
PF MVC (N.m)	$\bar{x}$	168.8	121.1	81.1	64.7
	SD	20.2	44.0	24.0	22.3
PF MVC/CSA ($N.m/cm^2$)	$\bar{x}$	4.7	3.93	2.88	3.05
	SD	0.82	1.58	0.67	0.73
N		5	5	5	5
Ages (Yr)		23-30	23-31	85-100	82-98

ANOVA Results

Combined CSA:

Sex Effect, $F=10.68$, $df=1,16$, $p<.005$

Age Effect, $F=24.68$, $df=1.16$, $p<.001$

PF MVC/CSA:

Sex Effect, $F=.433$, $df=1,16$, $p>.25$

Age Effect, $F= 8.81$, $df=1,16$, $p<.01$

Interaction effects were not significant

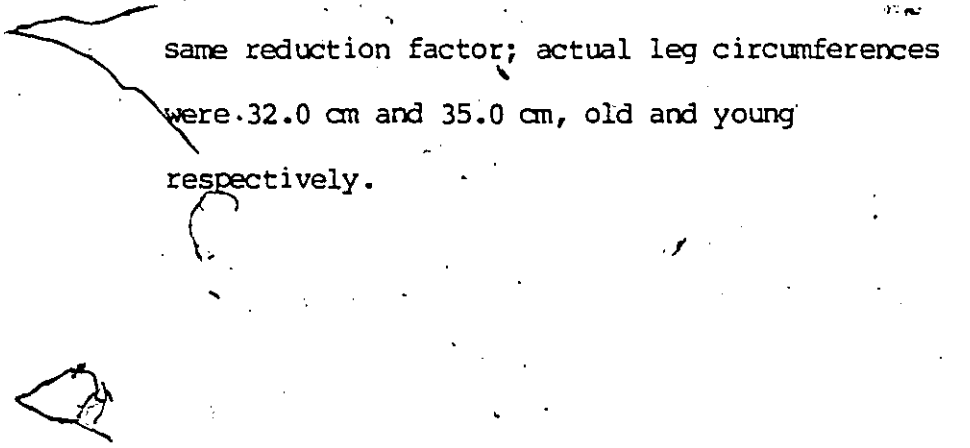


Figure 9. Ultrasound images of the lower leg of men aged 90 and 31 years. Both images have the same reduction factor; actual leg circumferences were 32.0 cm and 35.0 cm, old and young respectively.

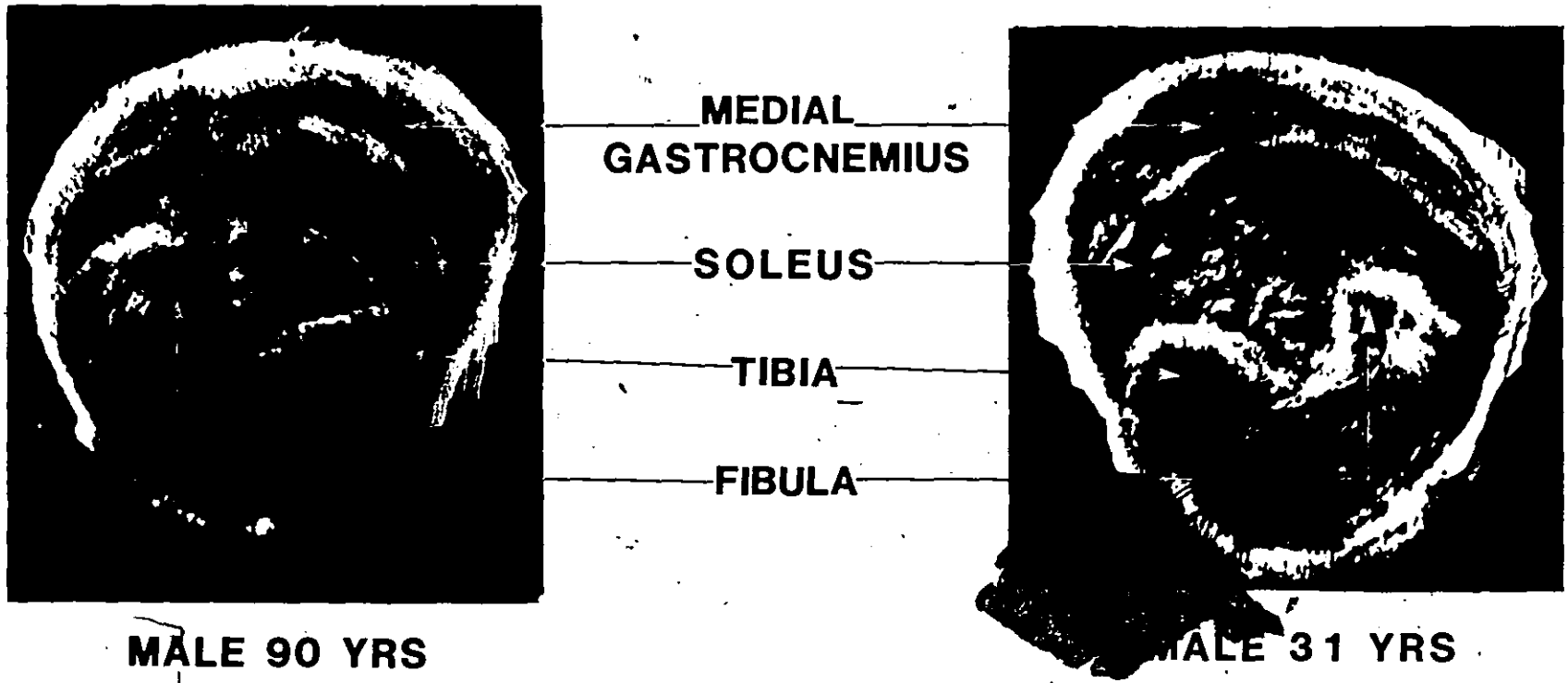
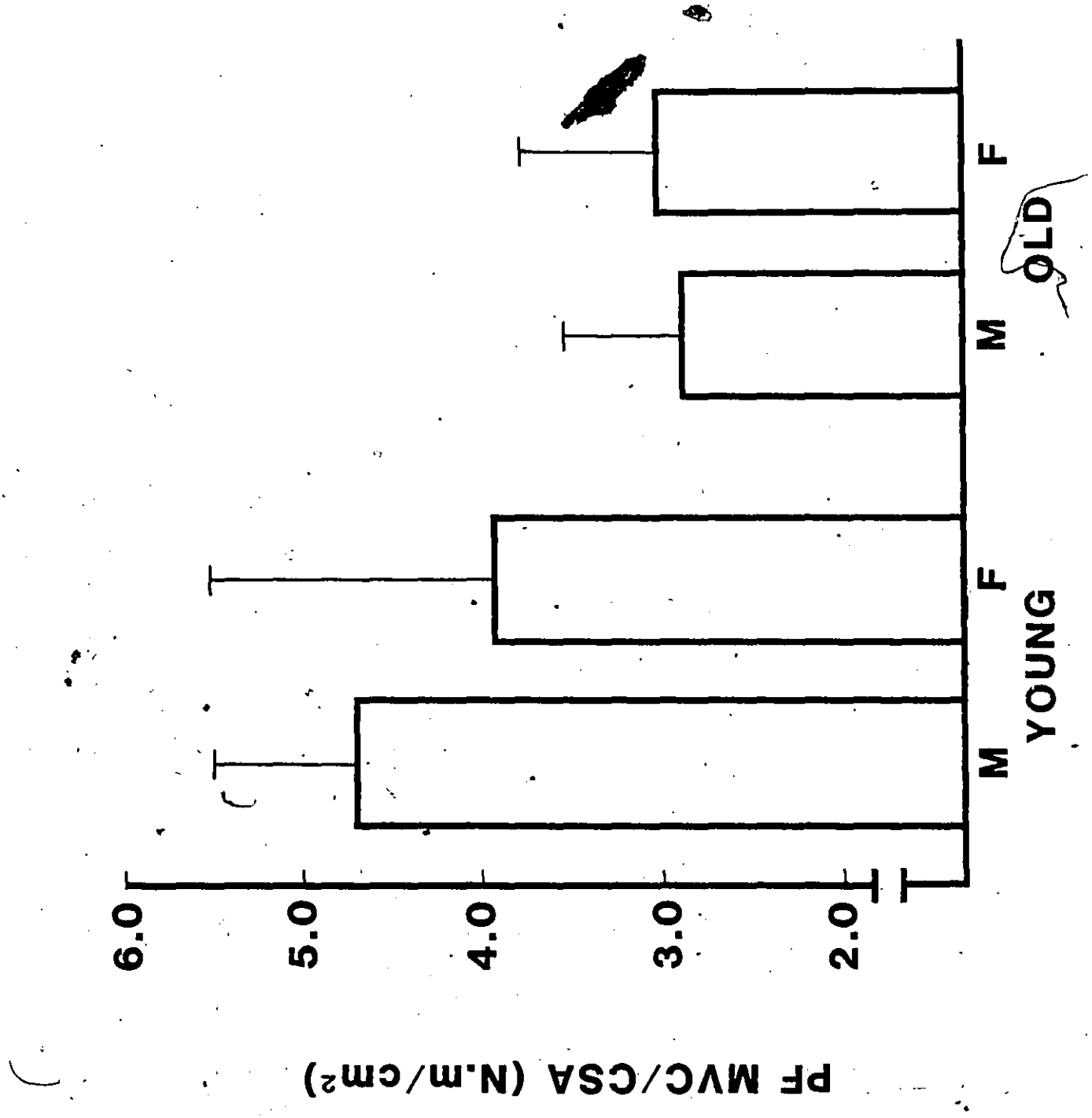

MEDIAL GASTROCNEMIUS
SOLEUS
TIBIA
FIBULA
MALE 90 YRS
ALE 31 YRS

Figure 10. PF strength relative to muscle CSA in young and old men and women. Cross-sectional areas (CSAs) of the soleus and gastrocnemius muscles were measured using ultrasound imaging. Young adults, aged 23 to 31 yr, had significantly higher ratios than old adults, aged 82 to 100 yr ($p<.01$). Sex was not a significant factor. Mean and 1 SD are shown, N = 5 per group.


PF MVC/CSA (N.m/cm²)
6.0
5.0
4.0
3.0
2.0
YOUNG
M
F
OLD
M
F

C. Isometric Twitch Characteristics of the Dorsiflexor and Plantarflexor Muscle Groups

Twitch characteristics of the dorsiflexor muscle group are shown in Table 6 (see Fig. 3 in the Methods chapter for a description of isometric twitch analysis). The ratio of peak twitch torque divided by the MVC value was included as an additional variable. Corresponding values for the plantarflexor twitch are given in Table 7. The data was grouped according to age and sex and statistical analyses of the main effects of these factors on dorsiflexor and plantarflexor twitch parameters are presented in Table 8.

M-wave and peak twitch torque. For both plantarflexor and dorsiflexor twitches, M-waves were significantly smaller in the older age groups (Fig. 11 and Table 8). This aging effect was most pronounced in the 80 to 100 yr old category. Males had larger plantarflexor M-waves than females; dorsiflexor M-waves were not significantly different between the sexes (Table 8). The peak twitch torque was also decreased in the older age groups. The effect of age was significant for both muscle groups, as was the effect of sex (Fig. 12). The influence of age seemed to be greater on the plantarflexor M-wave than on plantarflexor peak twitch torque (Table 7), whereas in dorsiflexor muscles there was closer agreement between changes in these two measurements across age groups (Table 6).

The ratios between peak tension and MVC in the dorsiflexor muscle group did not vary significantly between the sexes, nor systematically with advancing age (Table 6). The middle-aged groups had the highest

Table 6. Isometric Twitch Characteristics of the Resting DF Muscle Group

Variable	Sex		Age Group (Yr)				
			20-32	40-52	60-69	70-79	80-100
M-Wave (mv)	M	$\bar{x}$	9.4	9.7	7.0	7.8	5.4
		SD	2.6	1.5	1.9	3.1	1.6
	F	$\bar{x}$	9.1	10.5	7.9	6.3	5.2
		SD	2.6	2.3	4.0	2.8	2.0
P_t (N.m)	M	$\bar{x}$	4.2	4.5	3.3	3.3	2.6
		SD	1.5	1.2	1.4	1.3	0.8
	F	$\bar{x}$	2.7	3.7	2.8	1.8	1.7
		SD	1.3	0.9	1.0	0.9	0.8
P_t to MVC Ratio	M	$\bar{x}$	.096	.121	.092	.106	.109
		SD	.039	.034	.039	.033	.035
	F	$\bar{x}$	.098	.149	.119	.085	.104
		SD	.037	.046	.039	.035	.033
CT (ms)	M	$\bar{x}$	100.9	110.5	103.9	115.3	125.4
		SD	7.4	13.4	11.0	15.1	20.8
	F	$\bar{x}$	96.4	112.5	115.0	110.0	127.5
		SD	7.8	10.3	9.4	12.5	10.0
1/2 RT (ms)	M	$\bar{x}$	83.6	99.5	101.5	121.6	125.0
		SD	10.8	15.0	18.9	22.5	32.0
	F	$\bar{x}$	83.6	109.5	119.5	118.9	130.6
		SD	12.7	18.8	16.1	28.2	29.3

See Table 8 for ANOVA Results

Table 7. Isometric Twitch Characteristics of the Resting PF Muscle Group

Variable	Sex		Age Group (Yr)				
			20-32	40-52	60-69	70-79	80-100
M-Wave	M	$\bar{x}$	20.7	18.6	13.3	12.2	9.5
(mV)		SD	4.4	3.8	4.1	4.2	3.7
	F	$\bar{x}$	18.9	15.0	10.5	8.8	6.4
		SD	3.5	4.8	4.6	2.6	1.7
P_t	M	$\bar{x}$	15.5	16.3	13.4	13.4	11.9
		SD	3.8	3.5	4.2	4.1	2.3
(N.m)	F	$\bar{x}$	13.6	14.5	11.9	13.0	8.6
		SD	3.4	3.1	3.2	3.5	3.0
P_t	M	$\bar{x}$	.091	.096	.098	.114	.133
to MVC		SD	.017	.021	.021	.035	.021
Ratio	F	$\bar{x}$	.126	.116	.125	.148	.169
		SD	.036	.016	.019	.055	.037
CT	M	$\bar{x}$	143.6	168.5	169.6	177.8	185.8
(ms)		SD	13.3	16.3	13.3	19.3	22.1
	F	$\bar{x}$	146.4	179.0	181.5	182.8	195.0
		SD	20.6	8.4	10.6	23.2	26.9
1/2 RT	M	$\bar{x}$	108.6	122.0	116.5	133.1	144.2
(ms)		SD	12.3	14.2	16.5	33.3	21.2
	F	$\bar{x}$	123.2	138.5	133.0	142.8	168.8
		SD	12.1	13.8	20.6	26.6	30.1

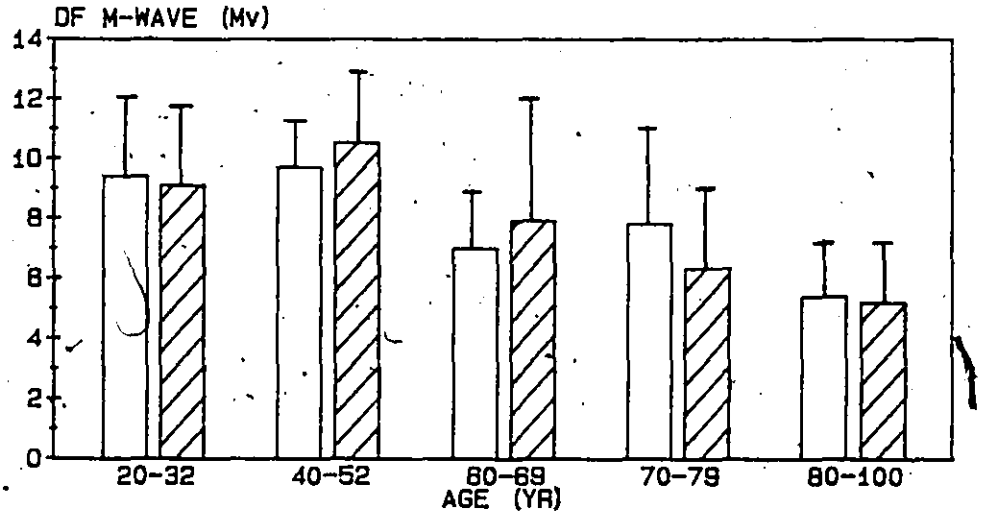
See Table 8 for ANOVA Results

Table 8. Effects of Age and Sex on DF and PF Twitch Characteristics: ANOVA Results

Variable	Factor			
	Age Group		Sex	
	F Ratio	p	F Ratio	p
DF Twitch				
M-Wave	10.99	<.0001	.02	=.8943
P_t	8.75	<.0001	21.11	<.0001
P_t/MVC	4.01	<.005	.73	=.3935
CT	12.47	<.0001	.19	=.6631
1/2 RT	13.23	<.0001	2.21	=.1404
PF Twitch				
M-Wave	32.32	<.0001	15.18	<.0005
P_t	6.35	<.0005	7.09	<.01
P_t/MVC	8.76	<.0001	28.61	<.0001
CT	18.85	<.0001	5.07	<.05
1/2 RT	10.41	<.0001	15.17	<.0005

df for Age Group = 4,101; df for Sex = 1,101
None of the interaction effects were significant

Figure 11. Compound muscle action potentials (M-Waves) of the DF and PF muscle groups recorded from men and women aged 20 to 100 yr. For DF muscles, sex was not a significant factor, but age group was ($p<.0001$). For PF muscles both variables were significant ($p<.0005$ for sex, $p<.0001$ for age group). Means and 1 SD are shown, N = 63M, 48F; range of 8 to 16 per group. Open bars = males.


DF M-WAVE (Mv)
14
12
10
8
8
4
2
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

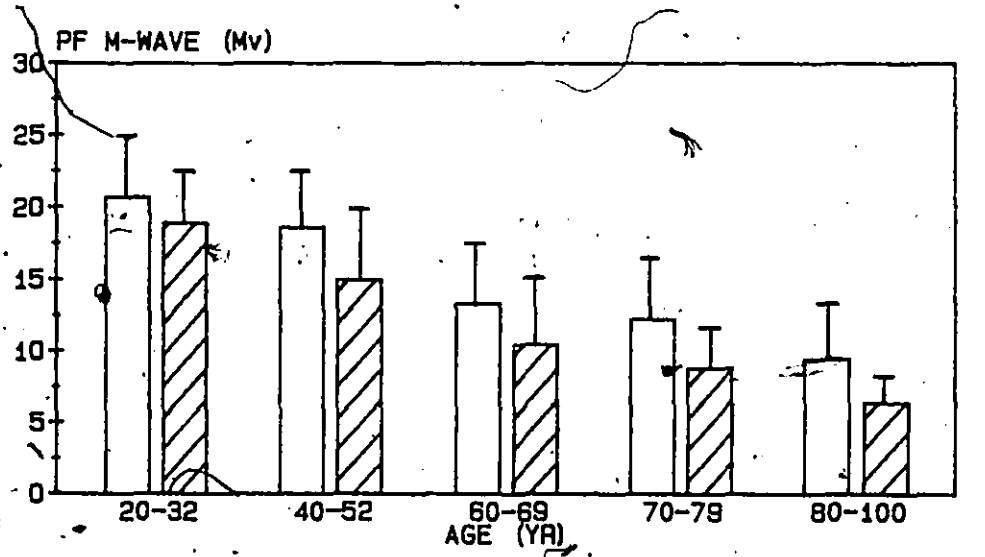
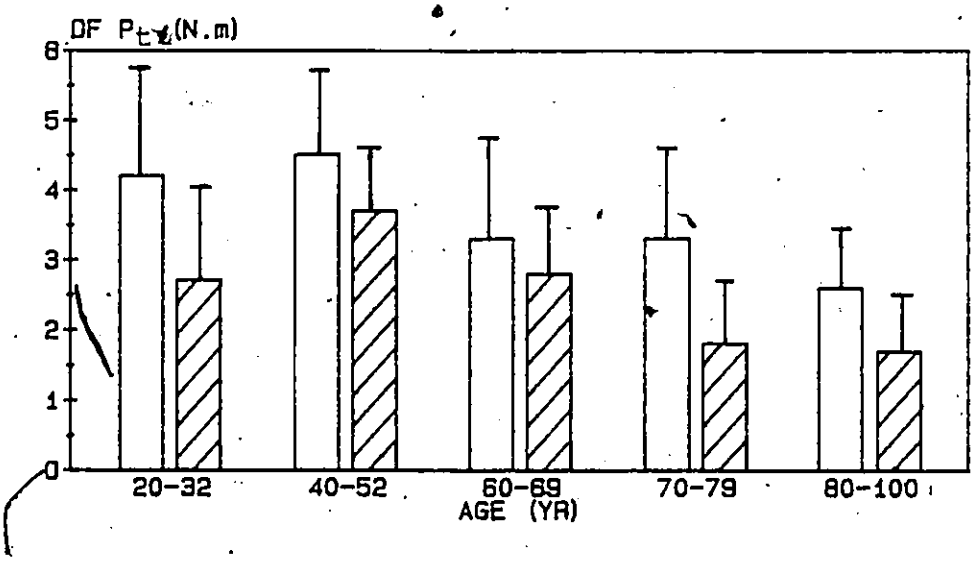
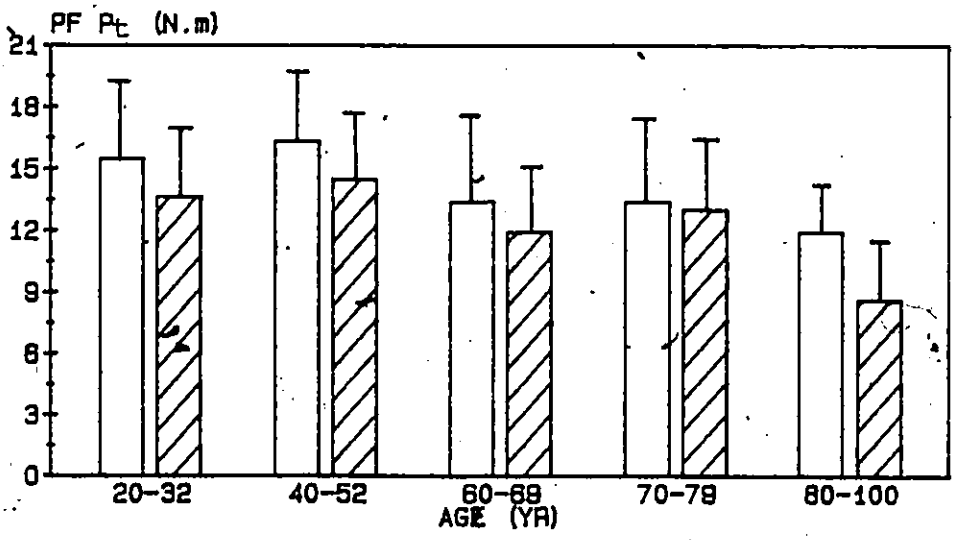

PF M-WAVE (Mv)
30
25
20
15
10
5
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

Figure 12. Peak torque (P_t) of the DF and PF isometric twitch in men and women aged 20 to 100 yr. Sex and age group were significant factors in both muscle groups (for DF, $p<.0001$ for both sex and age group; for PF, $p<.01$ for sex and $p<.0005$ for age group). Means and 1 SD are shown, N = 63 M, 48F; range of 8 to 16 per group. Open bars = males.


DF Pt (N.m)
8
5
4
3
2
1
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

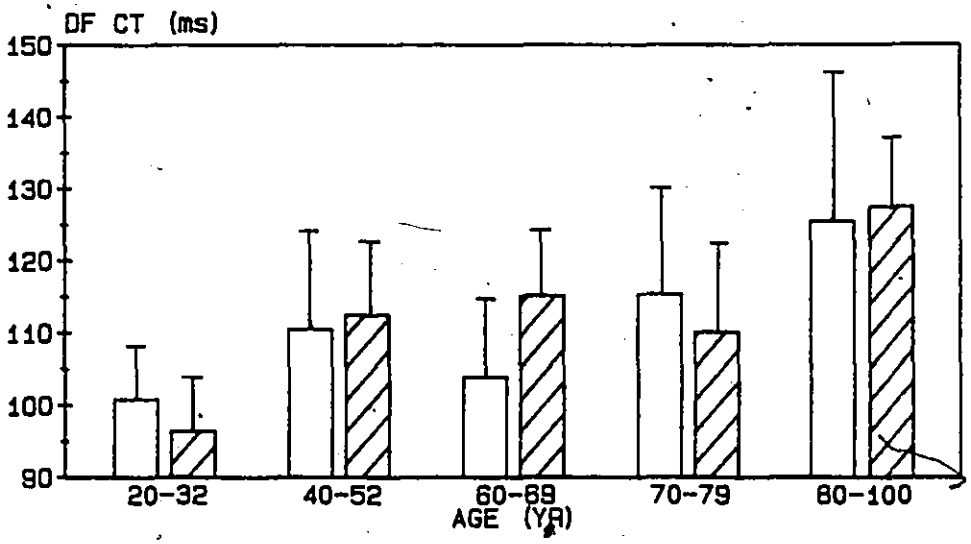

PF Pt (N.m)
21
18
15
12
9
6
3
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

mean values for this ratio. For the plantarflexor muscle group, increasing age had significant, positive effects on the ratio of peak twitch torque to MVC ($p<.0001$, see Tables 7 and 8). Females also had significantly higher ratios than males ($p<.0001$).

Twitch duration. Contraction time and one-half relaxation time of the dorsiflexor twitch were increased significantly with advancing age (see Tables 6 and 8, Figs. 13 and 14). There was no difference between the sexes in these parameters. For the plantarflexor twitch, contraction time and one-half relaxation time also increased significantly in the older age groups. In addition, females had significantly longer plantarflexor contraction times and one-half relaxation times than males (Tables 7 and 8). The plantarflexor contraction time was longer than the dorsiflexor contraction time in all age groups, as illustrated in Fig. 13. A similar observation was made when plantarflexor and dorsiflexor one-half relaxation times were compared (see Fig. 14).

Twitch times of the lateral gastrocnemius, medial gastrocnemius, soleus and plantarflexor muscles stimulated individually: comparisons between young and old men and women. The prolongation of plantarflexor twitch times with increasing age was studied in more detail by eliciting twitches of the lateral gastrocnemius, medial gastrocnemius and soleus muscles individually in young and old adults. Mean contraction times for these muscles, and for the plantarflexor twitch, were compared between 4 groups: males and females in young and old age categories. As illustrated in Fig. 15, the contraction times were significantly different between the muscles ($p<.0001$, see Table 9), but not between

Figure 13. Contraction time (CT) of the DF and PF isometric twitch in men and women aged 20 to 100 yr. For DF CTs, sex was not a significant factor, but age group was ($p<.0001$). For PF muscles both variables were significant ($p<.05$ for sex, $p<.0001$ for age group). Means and 1 SD are shown, N = 63 M, 48F; range of 8 to 16 per group. Open bars = males.


DF CT (ms)
150
140
130
120
110
100
90
20-32
40-52
60-69
70-79
80-100
AGE (YR)

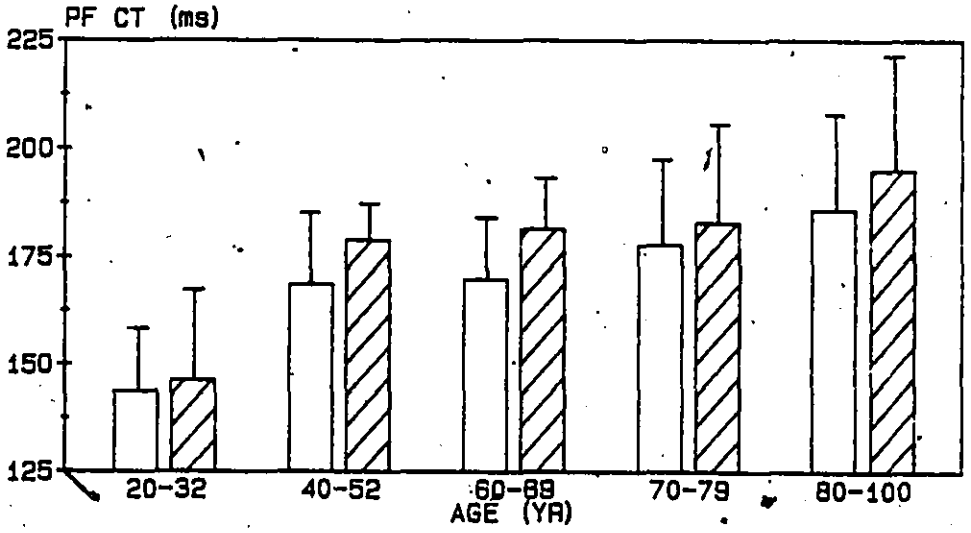
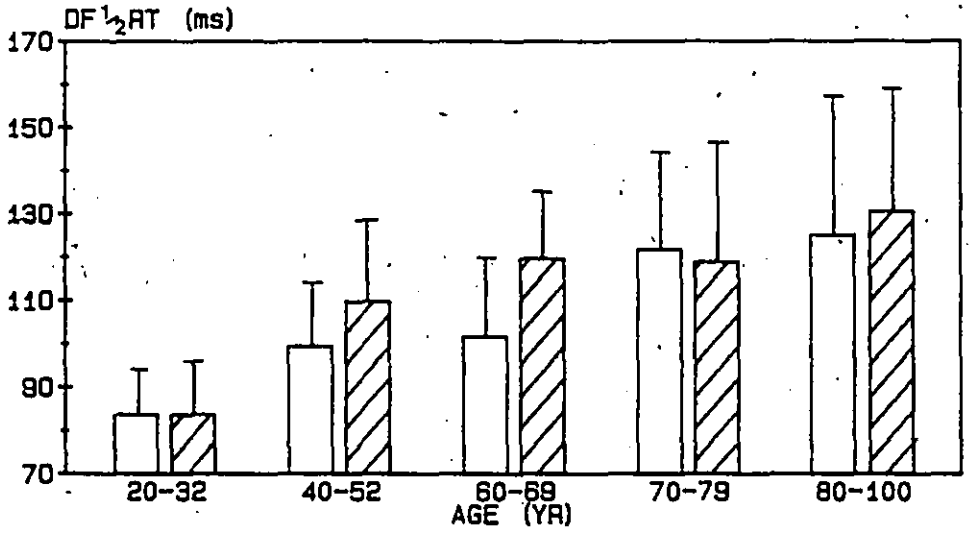

PF CT (ms)
225
200
175
150
125
20-32
40-52
60-69
70-79
80-100
AGE (YR)

Figure 14. One-half relaxation time (1/2 RT) of the DF and PF isometric twitch in men and women aged 20 to 100 yr. For DF 1/2 RTs, sex was not a significant factor, but age group was ($p<.0001$). For PF muscles, both variables were significant ($p<.0005$ for sex, $p<.0001$ for age group). Means and 1 SD are shown, N = 63M, 48F; range of 8 to 16 per group. Open bars = males.


DF ½AT (ms)
170
150
130
110
90
70
20-32
40-52
60-69
70-79
80-100
AGE (YR)

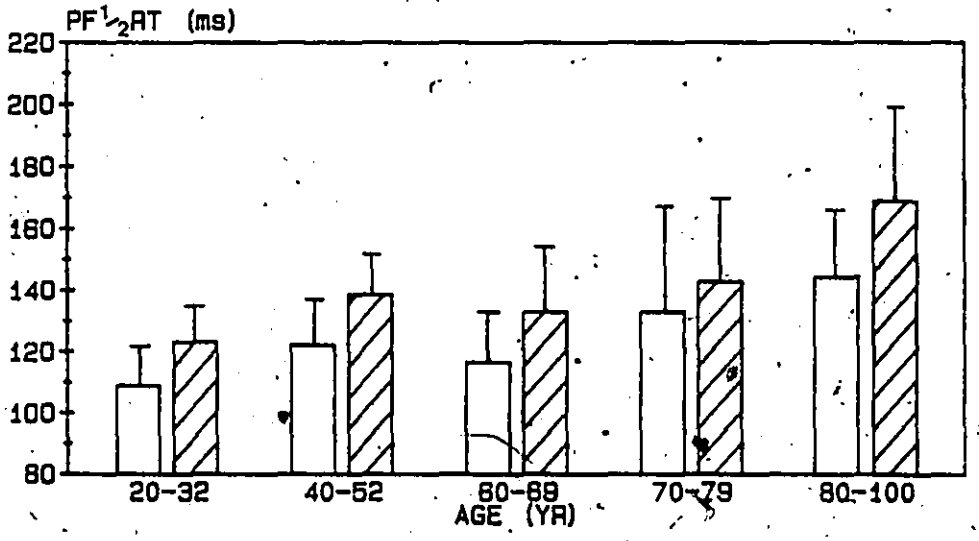

PF ½AT (ms)
220
200
180
160
140
120
100
80
20-32
40-52
60-69
70-79
80-100
AGE (YR)

Table 9. Twitch Times of the Individual Triceps Surae Muscles in Young and Old Adults

Muscle	Men		Women	
	Young	Old	Young	Old
	Contraction Time (ms)			
LG	93.3± 5.2	122.5±18.9	106.7± 8.8	116.4±17.0
MG	105.0±17.9	130.6±16.1	125.8±13.9	135.0±13.5
SOL	152.5±19.7	165.0±23.5	160.0±18.2	165.7±22.1
PF GROUP	139.2± 9.2	173.8±23.9	140.0±10.0	172.9±22.3
	1/2 RELAXATION TIME (ms)			
LG	84.2±21.3	117.5±19.8	113.3±15.4	145.0±42.5
MG	100.0±16.1	130.0±35.3	115.8±25.6	125.7±20.5
SOL	149.2±41.6	175.6±22.1	165.8±24.4	222.1±23.6
PF GROUP	115.8±15.9	133.8±28.6	125.0±17.6	145.0±23.8
N	6	6	8	7
Ages (Yr)	22-32	22-31	69-100	62-91

Values are mean ± SD

ANOVA Results

CTs:

Sex Effect, F= 1.07, df=1,23, p>.31
Age Effect, F=16.49, df=1,23, p>.0006
Muscle Effect, F=82.31, df=3,69, p<.0001
Age X Muscle, F= 3.49, df=3.69, p<.05
Other interaction effects were not significant

1/2 RTs:

Sex Effect, F= 6.87, df=1,23, p<.02
Age Effect, F=15.18, df=1,23, p<.001
Muscle Effect, F=50.79, df=3,69, p<.0001
Interaction effects were not significant

Figure 15. Contraction time of the lateral gastrocnemius (LG), medial gastrocnemius (MG), soleus (SOL) and entire plantarflexor (PF) muscle isometric twitch in young and old men and women. Significant differences were found: between muscles ($p<.0001$) and between age groups ($p<.0006$), with the exception of SOL CTs. Means and 1 SD are shown, N = 6 YG M, 8 OLD M, 6 YG F, 7 OLD F. Respective age ranges of young and old adults were 22-32 yr and 62-100 yr.

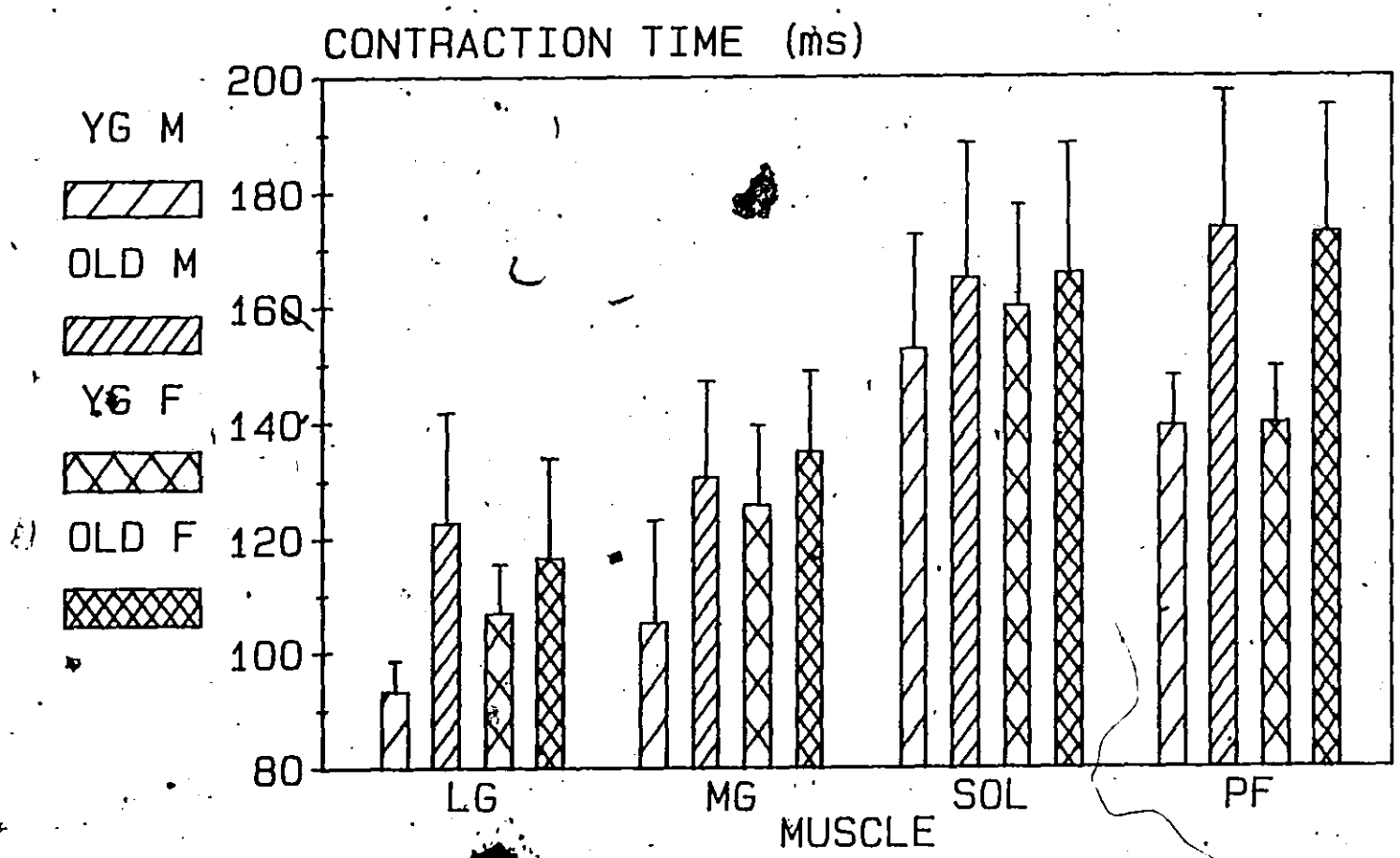
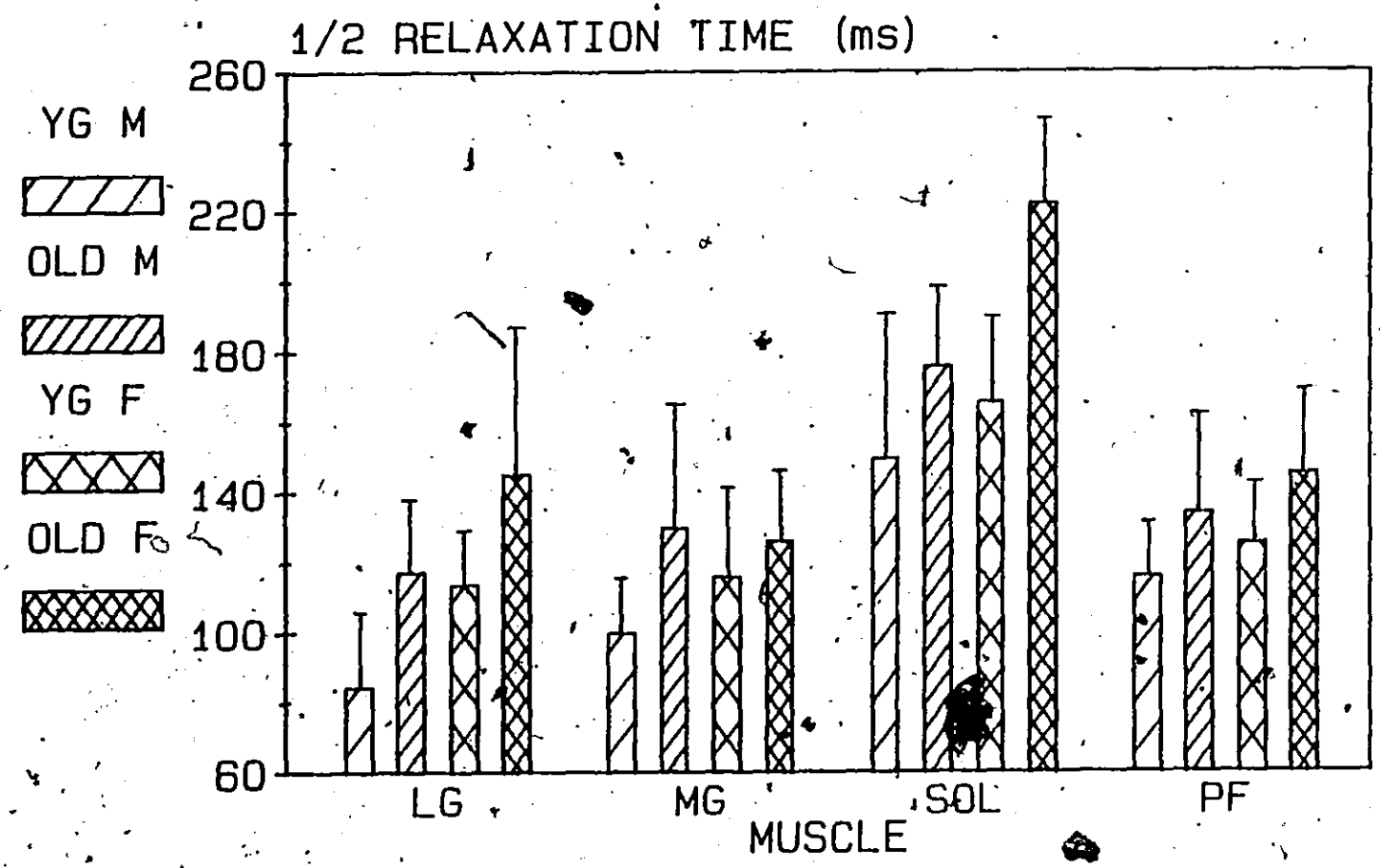

CONTRACTION TIME (ms)
200
180
160
140
120
100
80
YG M
OLD M
YG F
OLD F
LG
MG
SOL
PF
MUSCLE

Figure 16. One-half relaxation time of the lateral gastrocnemius (LG), medial gastrocnemius (MG), soleus (SOL) and entire plantarflexor (PF) muscle isometric twitch in young and old men and women. Significant differences were found: between muscles ($p<.0001$); between age groups ($p<.001$) and between sexes ($p<.02$). Means and 1 SD are shown, N= 6 YG M, 8 OLD M, 6 YG F, 7 OLD F. Respective age ranges of young and old adults were 22-32 yr and 62-100 yr.


1/2 RELAXATION TIME (ms)
260
220
180
140
100
60
YG M
OLD M
YG F
OLD F
LG
MG
SOL
PF
MUSCLE

the sexes. The older age group had significantly prolonged contraction times overall ($p<.0006$, Table 9), but the effect was not consistent across muscles (there was a significant interaction between age and muscle effects ($p<.05$), which indicated that the differences between young and old groups were less pronounced for some of the muscles than for others). Differences between mean contraction times in young and old groups were thus tested for significance in the case of each muscle with the Newman-Keuls multiple- range test; this analysis showed young and old soleus mean contraction times were not significantly different. Similar age-wise comparisons of lateral gastrocnemius, medial gastrocnemius and plantarflexor means revealed a significant age effect in each case ($p<.01$).

As shown in Fig. 16, old subjects had longer one-half relaxation times in the different muscles ($p<.0001$). In addition, females had significantly longer one-half relaxation times than males ($p<.02$, see Table 9). The soleus was distinct from the other muscles because of its prolonged one-half relaxation time (Fig. 16).

Potentiation of the isometric twitch. There was a striking effect of a brief (5s) MVC on a subsequent dorsiflexor twitch. As shown in Table 10, younger men produced the greatest absolute increase in twitch torque. Potentiation was also expressed relative to the resting twitch torque; average increases in peak twitch torque ranged between 67% for the youngest male group to 28% for women aged 70 to 79 yr (see Fig. 17). M-waves and contraction times of the potentiated twitches were not altered to any extent. One-half relaxation times were markedly reduced for potentiated twitches and the older age groups had the

Table 10. Comparison of the Resting and Potentiated DF Isometric Twitches

Sex		Age Group (Yr) 20–32	40–52	60–69	70–79	80–100
				M-Wave (mV)		
M	Mean	9.9	9.9	7.0	7.7	5.5
	Diff. Resting $\bar{x}$	+0.5	+0.2	0	-0.1	+0.1
F	Mean	9.4	10.7	8.0	6.7	5.4
	Diff. Resting $\bar{x}$	0.3	+0.2	+0.1	+0.4	+0.2
				Peak Torque (N.m)		
M	Mean	7.0	6.5	4.5	4.4	3.4
	Diff. Resting $\bar{x}$	+2.8	+2.0	+1.2	+1.1	+1.2
F	Mean	4.4	5.3	3.7	2.3	2.3
	Diff. Resting $\bar{x}$	+1.7	+1.6	+0.9	+0.5	+0.6
				Contraction Time (ms)		
M	Mean	98.6	106.0	103.9	108.8	119.8
	Diff. Resting $\bar{x}$	-2.3	-4.5	0	-6.5	-5.6
F	Mean	92.7	108.5	106.5	102.8	128.8
	Diff. Resting $\bar{x}$	-3.7	-4.0	-8.5	-7.2	+1.3
				One-half Relaxation Time (ms)		
M	Mean	67.7	81.0	81.5	95.0	104.1
	Diff. Resting $\bar{x}$	-15.9	-18.5	-20.0	-26.6	-20.9
F	Mean	67.3	93.5	85.0	86.1	116.9
	Diff. Resting $\bar{x}$	-16.3	-16.0	-34.5	-32.8	-13.7

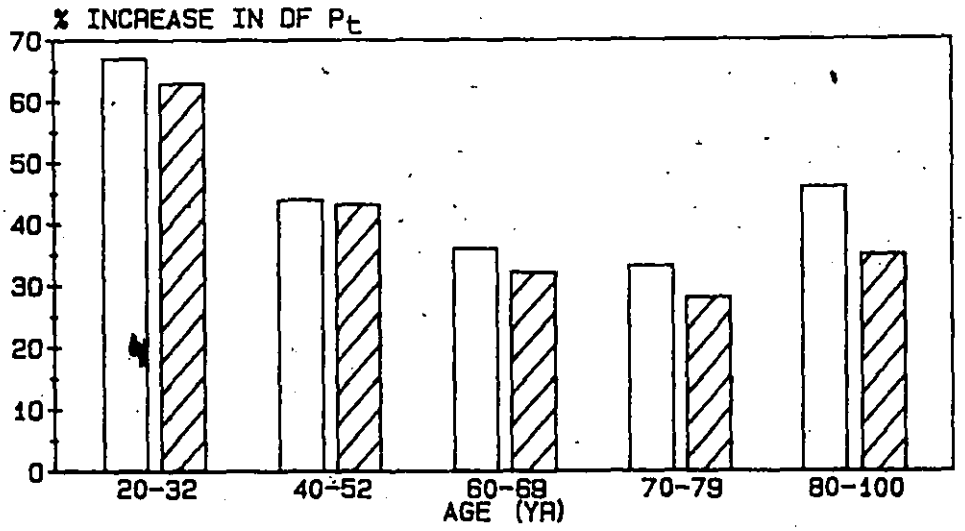
Note: Variances about the means were similar to resting twitch values.

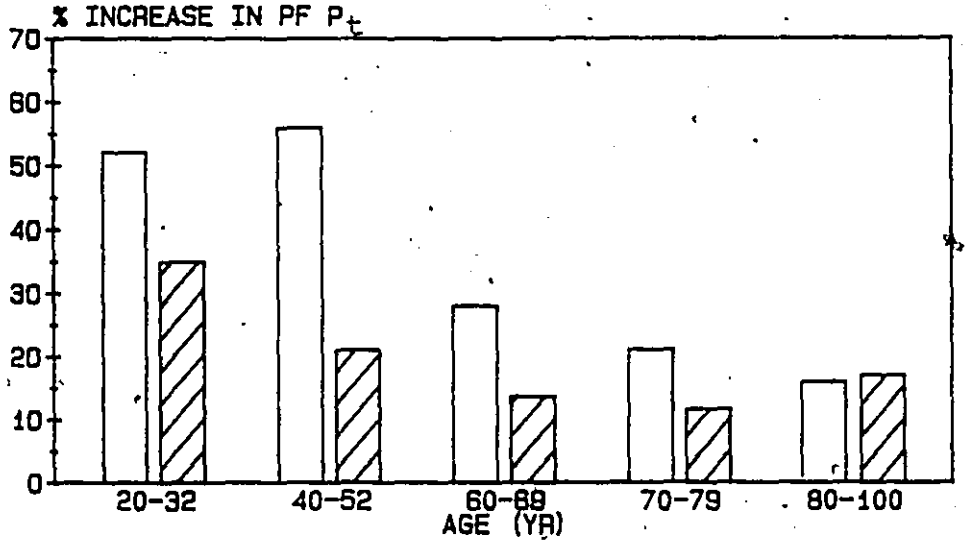
Table 11. Comparison of the Resting and Potentiated PF Isometric Twitches

Sex		Age Group (Yr) 20-32	40-52	60-69	70-79	80-100
		M-Wave (mV)				
M	Mean	20.7	18.6	13.4	12.5	9.7
	Diff. Resting $\bar{x}$	0	0	+0.1	+0.3	+0.2
F	Mean	20.1	15.0	11.1	8.9	6.7
	Diff. Resting $\bar{x}$	+1.2	0	+0.6	+0.1	+0.3
		Peak Torque (N.m)				
M	Mean	23.5	25.5	17.1	16.2	13.8
	Diff. Resting $\bar{x}$	+8.0	+9.2	+3.7	+2.8	+1.9
F	Mean	18.3	17.5	13.5	14.5	10.1
	Diff. Resting $\bar{x}$	+4.7	+3.0	+1.6	+1.5	+1.5
		Contraction Time (ms)				
M	Mean	131.7	149.5	149.2	149.7	161.7
	Diff. Resting $\bar{x}$	-11.9	-19.0	-20.4	-28.1	-24.1
F	Mean	134.6	167.0	156.5	160.6	171.4
	Diff. Resting $\bar{x}$	-11.8	-12.0	-25.0	-22.2	-23.6
		One-half Relaxation Time (ms)				
M	Mean	93.8	112.0	101.2	114.1	124.9
	Diff. Resting $\bar{x}$	-14.8	-10.0	-15.3	-19.0	-19.3
F	Mean	114.4	123.8	115.0	120.4	146.3
	Diff. Resting $\bar{x}$	-11.8	-14.7	-18.0	-22.4	-22.5

Note: Variances about the means were similar to resting twitch values.

Figure 17. Potentiation of the peak torque (P_t) of the DF and PF isometric twitch following a 5s MVC in men and women aged 20 to 100 yr. Percent increases were calculated with respect to mean P_t of the resting twitch, see Fig. 14. N = 63M, 48F, range of 8 to 16 per group. Open bars = males.


% INCREASE IN DF P_t
70
60
50
40
30
20
10
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)


% INCREASE IN PF P_t
70
60
50
40
30
20
10
0
20-32
40-52
60-69
70-79
80-100
AGE (YR)

greatest absolute decreases. Relative changes were all in the range of 15% to 30%.

Potentiation of the plantarflexor twitch resulted in absolute peak twitch torque increases which were consistently greater than those for the dorsiflexor muscle (compare Tables 10 and 11). However, after normalization of values with respect to the resting twitch, the increase in peak twitch torque was usually greater for the dorsiflexor muscle (Fig. 17). Those with the largest resting twitches produced the greatest twitch potentiation. Thus, males aged 40 to 52 yr had the highest average increase: 9.2 N.m or 56%. M-waves of the potentiated plantarflexor twitch were not different from resting values.

Both contraction times and one-half relaxation times were decreased in the potentiated twitches of the plantarflexor muscles (Table 11). Like the dorsiflexor muscle, twitch durations were reduced to a greater extent in the oldest subjects. Averaged relative changes were between 8% to 15%. In summary, potentiation of the older person's muscle resulted in a twitch that was much more like that of resting young adult muscle; tension development had become higher and more rapid (compare young adult resting twitch parameters in Tables 6 and 7 to values for the potentiated twitch of old adults in Tables 10 and 11, respectively).

Passive tension at 30°P and 10°D. The amount of passive tension generated by stretching the dorsiflexor and plantarflexor muscle groups to their respective test positions is given in Table 12. Age group was not a significant factor for either muscle. Females developed significantly less passive tension than males when the dorsiflexor

Table 12. Passive Tension about the Ankle Joint at 30°P and 10°D

Sex		Age Group (Yr) 20-32	40-52	60-69	70-79	80-100
		At 30° of Plantarflexion (N.m)				
M	$\bar{x}$	2.3	1.8	2.4	2.0	2.3
	SD	.9	.7	.9	.7	.7
F	$\bar{x}$	1.4	1.3	1.8	1.6	1.3
	SD	.3	.4	.7	.4	.4
		At 10°D of Dorsiflexion (N.m)				
M	$\bar{x}$	3.1	3.4	3.5	2.8	2.8
	SD	1.0	1.0	2.1	1.1	1.3
F	$\bar{x}$	2.2	2.6	2.7	2.9	2.8
	SD	0.8	1.1	1.0	0.9	1.0

ANOVA Results

At 30°P:

Sex Effect, $F=22.22$, $df=1,101$, $p<.0001$

Age Group Effect, $F= 1.90$, $df=4,101$, $p=.117$

At 10°D:

Sex Effect, $F= 3.89$, $df=1,101$, $p=.051$

Age Group Effect, $F= .53$, $df=4,101$, $p=.717$

Interaction effects were not significant

muscle-tendon complex was stretched to 30°P ($p<.0001$). The sex difference in passive tension developed by the plantarflexor complex was not statistically significant ($p=.0513$). Mean values for passive tension across age groups were always greater in the case of the plantarflexor muscle-tendon complex.

D. Flexibility of the Ankle Joint

The extent to which the ankle could be dorsiflexed decreased with advanced age ($p<.0001$); there was no significant difference between the sexes in this variable (Table 13). However, even the oldest subjects had considerable flexibility at the ankle (Fig. 18); on average, their joints could be dorsiflexed by 30° from the neutral position (sole of foot perpendicular to tibia). This limit was the point at which subjects felt their ankle could undergo no further rotation, despite the investigator's assistance in moving it. Most older individuals could also rotate their ankle into at least 40° of plantarflexion.

Table 13. Effects of Age and Sex on Passive Range of Ankle Joint Movement

		Degrees of Dorsiflexion from Horizontal				
		Age Group (Yr)				
		20-32	40-52	60-69	70-79	80-100
Males	$\bar{x}$	35.6	32.9	29.9	30.8	30.8
	SD	5.7	4.5	6.7	6.8	4.8
Females	$\bar{x}$	37.7	34.7	30.4	27.2	26.[illegible]
	SD	3.7	5.0	6.7	5.8	3.9

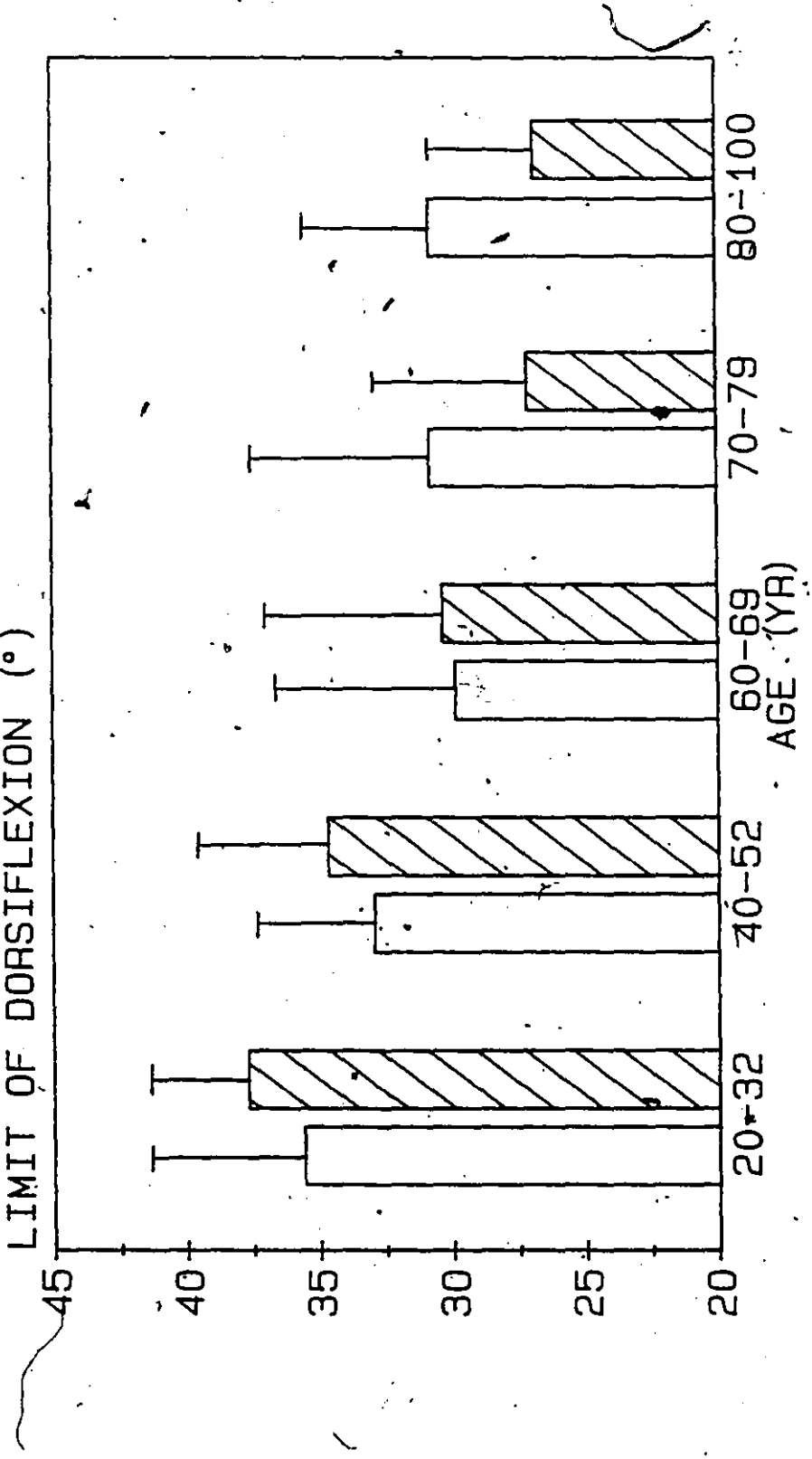
ANOVA Results

Sex Effect, F= .30, df=1,101, p=.587

Age Group Effect, F=8.07, df=4,101, p<.0001

Interaction effect was not significant

Figure 18. Limit of dorsiflexion in men and women aged 20 to 100 yr. The effect of age group was significant ($p<.0001$) on the degrees of dorsiflexion to which the ankle could be rotated from the neutral position. Sex was not a significant factor. Means and 1 SD are shown, N = 63M, 48F, range of 8-16 per group. Open bars = males.


LIMIT OF DORSIFLEXION (°)
45
40
35
30
25
20
20-32
40-52
60-69
70-79
80-100
AGE (YR)

IV. DISCUSSION

A. Relationship between Voluntary Strength and Age

Decreases in voluntary strength with aging generally did not begin until the sixth decade in this sample of healthy adults. In terms of absolute torque production, plantarflexor MVC decreased much more than dorsiflexor MVC with advancing age. The decline in strength with aging was greater for men than women in both muscles, but in all age groups men had higher mean values. When the data was normalized with respect to young adult means, the relative effect of increasing age was similar on both muscles. Females generally showed less relative change than men, except for plantarflexor values in the oldest group of subjects.

Normalization of the data allowed for comparisons with other studies of the relationship between age and strength in various muscles. First, the observation that plantarflexor MVC was not decreased in middle age, relative to young adults, is consistent with the results of Fugl-Meyer et al. (1980) and Belanger et al. (1983), who also examined the plantarflexor muscle group. A similar conclusion was reached in investigations of muscles in the hand, arm and shoulder, and upper leg (Shephard, 1969; Shock and Norris, 1970; Petrofsky and Lind, 1975; Montoye and Lamphiear, 1977; Larsson et al., 1979; Agnew and Maas, 1982). The nature of the relationship between adult age and function is somewhat controversial, because Asmussen et al. (1975) reported in their longitudinal study that middle-aged subjects did have significantly reduced handgrip strength when comparisons were made to

their values at a younger age. Changes in activity pattern might explain this difference and a more rigorously controlled longitudinal study would be necessary to resolve the issue. Such an investigation would be particularly valuable if several muscle groups were assessed. In the present research, an attempt was made to match groups of subjects at different ages with regard to several factors which might influence strength. These factors are discussed in more detail below.

MVC of subjects aged 60 to 100 yr. Several investigators have reported a difference in strength between young adults and people in the seventh decade; when these results are compared to values of the present study, less change was found with aging in the latter (average = 15%). For example, Fugl-Meyer et al. (1980) reported their group of 60 to 65 yr old men and women had, an average, 23% lower plantarflexor strength, relative to young adults. Davies et al. (1983) found mean plantarflexor MVC to be 43% less in a group of men with an average age of 69 yr (± 1.4, SD), when compared to a group of young men. Other values for differences between young and older groups, with varying age ranges in the latter, tend to fall between these extremes (see Table 1 in the Introduction chapter).

Some of the discrepancy between studies can be explained on the basis of how much size differed between young and old subjects. In selected samples of the population, body size can vary considerably among groups. Some authors, such as Shock and Norris (1970), and McDonagh et al. (1984), have applied correction factors of 8% and 18%, respectively, to their data. These corrections were meant to allow for the lower weights of the older men in the former study, and the lower

heights of the older men in the latter. In the present study, body size was similar in the various age groups. Thus, size variation did not add to the differences in strength between young and older adults (the 80 to 100 yr olds tended to be somewhat smaller in stature, but this point is clarified later in the Discussion). Men were taller than women at all ages (see Table 2 of the Methods chapter); therefore, differences between the strength of males and females included a component due to the lesser female size.

Subjects in the oldest age group still had about 50% of the strength of young adults, despite the fact their average age was 88 yr. This group consisted of survivors, who had lived longer than the average life expectancy. Their results fell along the regression line of strength versus age, made in the group of people aged 60 yr or older. It is noteworthy that, even though very old females were considerably weaker than young women, the two groups had similar body weights to support and control.

B. Possible Explanations for the Decreased Strength of the Aged

(1) First hypothesis: Old subjects' muscles were weak due to inactivity. One factor known to decrease voluntary strength is extreme inactivity such as that caused by limb immobilization (Sargeant et al., 1977; MacDougall et al., 1980; Sale et al., 1982; Davies and White, 1983a). A possible explanation for the decreased strength of the aged is that their habitual activity pattern was widely different from the younger adults, thereby creating disuse atrophy of the musculature. There are several reasons why this hypothesis is unlikely.

First, all subjects were screened to ensure that they had a daily activity pattern which included exercise of the ankle muscles obtained during walking and standing. The muscles acting at the ankle joint were particularly suited for this investigation because of their important role in locomotion and in maintaining the upright human posture (Joseph

and Nightingale, 1952; Winter, 1981). Subjects in the young and middle-aged groups were selected only if they were not engaging in high-resistance exercise programs to increase strength. Flatten and Rice (1982) have reported little change with age in the extent to which subjects engaged in low force, endurance types of activity in their sample of 30 to 95 yr old male and female volunteers living in the community in an American city. Their subjects were similar to those in the present investigation and it seems likely that activity levels were reasonably consistent among the various age groups examined herein.

An additional consideration is that during normal activity, old people were actually using a greater percentage of their maximal strength than young adults, because absolute strength was reduced in the elderly. Hence, the training benefits from daily activity should be higher in the elderly. Unfortunately, a validated instrument has not been developed for precise quantification of the amount of habitual activity which would specifically enhance muscle strength. Available techniques like activity questionnaires and pedometers are sensitive to low-resistance, prolonged exercise which mainly influences cardiorespiratory endurance (Laporte et al., 1983).

Gutmann and Hanzlikova (1972) have concluded in an extensive review of the literature dealing with aging and neuromuscular function that the muscle wasting associated with aging does not resemble disuse atrophy but is a unique form which they designated as senile atrophy. Muscle fibres are lost with aging but not lost following immobilization. Furthermore, disease seems to cause a reduction in plantarflexor twitch times (Davies and White, 1983a), rather then the prolongation observed with aging in the present study. It should also be noted that activity cannot be the only influence on muscle function because some motor units are very rarely recruited during normal activity (Hannerz, 1974; Grimby, 1984). Other factors, such

as neurotrophic substances (see Pette, 1980), must be involved in the regulation of normal muscle mass.

A valuable experiment on this question would be to test a group of aged competitive weight-lifters to observe whether strength was reduced relative to a similar group of young weight-lifters. It would also be of interest to determine whether high-resistance training can increase neuromuscular function in the elderly. Fries and Crapo (1981) have postulated a large capacity exists for increasing "vigour" in the later part of life if individuals adopt appropriate training strategies to elevate themselves above the normal curve of functional decline with aging. There is some evidence in the literature which indicates that exercise programs can lead to increased strength in the elderly (Perkins and Kauser, 1961; Moritani and deVries, 1980; Aniansson and Gustafsson 1981). However, a comprehensive investigation of the effects of strength training on the elderly neuromuscular system has not been published.

It is not known whether old muscle fibres retain the capacity to hypertrophy in response to increased demands for tension development; the training effects observed in the recent studies of Moritani and de Vries (1980) and Aniansson and Gustafsson (1981) were attributed to adaptations in the nervous system, not in muscle itself. Unfortunately, Moritani and deVries (1980) did not directly examine muscle fibres in their investigation. Aniansson and Gustafsson (1981) observed little change in the size of aged vastus lateralis muscle fibres with training, but subjects performed calisthenics, rather than high resistance exercise. It is possible that their program was not strenuous enough to stimulate muscle growth.

(2) Second hypothesis: Old subjects did not fully activate lower motor neurons during MVC. The hypothesis that old people were either unable

or unwilling to exert themselves as strenuously as young adults was not supported. The use of the interpolated twitch during MVC showed that old people generally achieved full activation of lower motor neurons. This was true in all cases for the dorsiflexor muscles and in most cases for the plantarflexor muscles. Belanger and McComas (1981) also observed that some young adults had difficulty in eliminating interpolated twitch increments during plantarflexor MVC trials, whereas during dorsiflexor MVC tests full activation was routinely achieved.

The group of old people selected for this study had intact motor pathways between the brain and muscles tested. Davies et al. (1983) reported that tetanic (involuntary) muscle contraction produced the same plantarflexor torque, relative to MVC, in old men as it did in young men. Their findings suggested that this select group of old men, who submitted to tetanic stimulation, apparently achieved motor unit activation levels equal to those of young men. The present study gave original observations on a large group of elderly men and women and showed most were able to achieve full motor unit activation. Even individuals with interpolated twitches present during plantarflexor MVC were close to a full activation pattern. The neural pathways used were among the longest in the body and despite reports of brain atrophy with aging (see Jones, 1983 for review and Anderson et al., 1983), functional evidence of lesions was not found in this part of the motor system in the present study. It might be argued that minor degeneration in descending motor pathways could have been concealed by a large safety-margin for motor unit activation. However, the inability of some young subjects to activate their plantarflexor muscles fully indicates that, for this muscle at least, there is

effectively no safety-margin; therefore, such an explanation for the findings in the elderly is not valid.

The old people in this study were apparently making optimal use of their muscle tension-generating capacity, according to the observed lack of any increase with the interpolated stimulus. As noted in the Methods chapter, the interpolated twitch technique was also used to motivate them during measurement of voluntary strength. Several attempts at MVC were made by all subjects, and in some cases a striking increase was registered over the first few trials. It was concluded that isometric strength testing can be used for safe, reliable estimates of muscular strength even in the very old, providing adequate time and explanation is allowed for in the testing procedure (see Appendix C). Concern that submaximal efforts might be given in isometric strength tests (eg. Jones, 1962; Krbemer and Marras, 1980) can be alleviated by use of the interpolated twitch procedure. The observation that voluntary strength could be markedly increased by repetition in some of the elderly, suggests that simple exercise programs could be effective in increasing the work capacity of such individuals.

(3) Third hypothesis: old subjects had smaller stature. Differences in size were minor between young and old adults, except for the group of 80 to 100 yr old subjects. In a randomly chosen group of adults that included four generations, a larger decrease in height with advancing age might be expected (Tanner, 1978), but the present study sample was a selected, more homogeneous group. The difference in strength in people of different heights is presumably due to the advantage of a greater cross-sectional area and an increased lever arm length in the

muscles of a tall person with long limb bones, if geometrical similarity among people of different stature is assumed (Haxton, 1944; Asmussen, 1968; Ikai and Fukanaga, 1970; Watson and O'Donovan, 1977; Smidt and Roger, 1982; Schantz et al., 1983; McCullagh et al., 1984). However, it may be that old people who are shorter have similar leg lengths to young adults and differences in stature are accounted for by shrinkage of the trunk length, apparently caused by a narrowing of the intervertebral spaces and an increased curvature of the upper spine (Fugl-Meyer et al., 1980; Steinberg, 1983). Therefore, the differences in height between the age groups in this study are likely of minor importance, perhaps even in the group of the oldest subjects.

(4) Fourth hypothesis: old subjects had less contractile tissue in their muscles. It is apparent that subjects aged 60 yr or more were generally weaker than young or middle-aged adults. The explanation for this observation is that they had less muscle tissue in their lower leg than younger adults, since levels of motor unit activation were generally similar across age groups. Hence, measurement of voluntary strength provided an accurate estimate of the amount of excitable mass present. Body weight, on the other hand, was not consistently reduced in the elderly subjects, nor was the circumference of the aged lower legs used in the ultrasound experiment.

Mean cross-sectional area of the gastrocnemius and soleus muscles was significantly less in the group of very old people examined, as compared to young adults. This finding explained part of the difference in strength between these groups. However, maximum plantarflexor strength values were reduced in the elderly subjects more

than their muscle cross-sectional areas, and hence, their mean ratio of strength per cross-sectional area was significantly decreased. Heights were equivalent for these selected subgroups of the subjects. Young and co-workers, who also used ultrasonic imaging methods, reported similar findings for the effects of aging on male quadriceps muscle - strength was more reduced than cross-sectional area in old men (Stokes et al., 1983). The effect was different in old women; they had equivalent decreases in strength and quadriceps cross-sectional area, when compared to young women (Young et al., 1982).

Fat and connective tissue may have replaced contractile material in the muscles of the elderly, thus occupying a greater relative proportion of the ultrasound images of leg cross-sections in old subjects as compared to young. Due to this replacement of one tissue by another, the old person's muscle belly may appear to have only a minor degree of atrophy when examined from the exterior. Several authors have noted in a qualitative manner that increased fat infiltration is present in aged muscle (Lowry et al, 1942; Verzar, 1959; Jennekens et al., 1971; Bulke et al., 1979; Borkan et al., 1983; Lexell et al., 1983), but precise quantification of the relative amounts of muscle vs other types of tissue in human or animal limbs has not yet been attempted in studies of the aging process. Although examination of cadervic material is one possible way of answering this question, there is always the drawback of not knowing the exact health status of the individual before death. Accurate, non-invasive quantification of the composition of healthy human tissue may be possible in the future with improved CAT-Scan techniques or with advanced nuclear magnetic resonance technology (there is currently much

interest in using these techniques for the assessment of muscle wasting in neuromuscular diseases such as muscular dystrophy, e.g. Brenton et al., 1981).

Whole-body muscle mass was estimated to be 45% lower in very old men (mean age of 90 yr), as compared to young men, according to measurements of creatinine clearance by Tzankoff and Norris (1977). This figure agrees closely with the difference in strength between very old and young men in the present study. Indeed, comparisons of apparent muscle mass over each decade from the third to the tenth reported by Tzankoff and Norris agree well with the corresponding age differences in strength in the present investigation.

Borkan et al. (1983) found a group of men aged 59 to 76 yr (mean was 69.4 yr) to have about 12.4% and 11.7% less muscle cross-sectional area in the upper leg and upper arm, respectively, than young men. They utilized the CAT-Scan technique to measure cross-sectional areas. The strength data from the present study, and from other investigators (see Table 1), would seem to suggest a greater difference in muscle mass for subjects tested in these age ranges. It is possible that radiologic investigation of muscle mass may tend to overestimate values for old adults, whether ultrasound or CAT-Scan techniques are used.

Compound muscle action potential. Overall, a decrease was observed in the size of the M-wave recorded from dorsiflexor and plantarflexor muscles in older subjects. These changes approximated the reductions in voluntary strength with aging, e.g. the oldest group had mean M-wave values of between 34 to 57% of the young adult means. Campbell et al. (1973) observed decreased M-waves from the extensor digitorum brevis (EDB) muscle in their sample

of subjects aged 60 to 96 yr and they attributed this finding to a progressive decrease with aging in the number of functioning motor units. Motor neurons are apparently lost with aging, according to counts of lumbrosacral anterior horn cells (Tomlinson and Irving, 1977); in addition, dysfunction occurs in other motor units (McComas, 1977).

In the present study, decreased motor unit counts were also found in the soleus muscles of 5 very old people (80-100 yr) examined by A.J. McComas, originator of the counting technique (McComas et al., 1971). The average motor unit count in soleus was 283±83 for these subjects, which represents a 70% reduction from the mean for young and middle-aged adults (McComas, 1977: 52). This change is less than the decrease in EDB counts found in the group of elderly people examined by Campbell et al. (1973). This pilot study was not expanded, but it would be of interest in a future investigation to compare soleus motor unit counts to those for the EDB muscle in the same subjects. The distal location of the EDB muscle necessitates longer motor neurons which may be more susceptible to peripheral neuropathy (Cavanagh, 1964; Sabin, 1982). With regard to aging in animals, Caccia et al. (1979) have reported similar findings of decreased M-waves and motor unit counts in the soleus muscles of aged rats and mice, when compared to young controls.

The correspondence between the M-wave and strength was not exact in the present study. Other factors, such as geometry of the muscle, and conductance of the skin, fat and connective tissue may have varied among age groups. Differences between men and women in these factors may explain why females had disporticnately high M-waves relative to

their strength, when compared to males.

Peak tension of the isometric twitch. Another indicator of the amount of excitable muscle tissue present is the peak tension generated during a maximal muscle twitch. Reduced peak twitch torque was found in the twitches of older age groups for both dorsiflexor and plantarflexor muscles. For the dorsiflexor muscles, the relationship between twitch tension and voluntary strength, expressed as the ratio of peak twitch torque to MVC, was similar across age groups. However, in the plantarflexor muscle this ratio increased with advancing age. One explanation for this change is that because the twitch duration also increased in the older groups, more time for tension development was present in twitches of old muscles. This factor would also explain why females had higher plantarflexor peak twitch torque to MVC ratios than males. Perhaps aging did not have the same effect on this ratio in the case of the dorsiflexor muscles because twitch duration was not increased in older age groups to the same extent.

Altered tissue elasticity may have also been a factor in changing plantarflexor peak twitch torque to MVC ratios. The absolute passive tension of the plantarflexor muscle-tendon complex did not vary systematically with increasing age. However, relative passive tension, expressed as a percentage of the total tension developed by the muscle during active contraction, was greater in the elderly. Therefore, in proportion to the amount of excitable mass present, old people did appear to have greater stiffness in the tissue making up the series elastic element. This change seems to represent a compensatory effect of aging because the efficiency of tension development is improved with

a less compliant series elastic element.

Implications of the change in excitable muscle mass. Despite the possibility that old muscles had become adapted for enhanced tension transmission, the average rate of force development during the twitch was clearly slowed with increased age. For example, very old plantarflexor muscles may take as long as 190 ms to produce a twitch torque of 10 N.m, whereas a young adult muscle may only require 100 ms to achieve the same effect. This difference may be functionally important during protective, reflex muscle contractions. In such situations rapid tension development may prevent trauma such as falling - a common problem for the elderly (Cape, 1978; Greenwood and Hopkins, 1982; Woollacott et al., 1982).

The decline in muscle mass with aging may be caused by a loss of cells; an average decrease of 24% in the estimated number of muscle fibres in the vastus lateralis muscle was found when old men aged 70 to 73 yr were compared to young men by Lexell et al. (1983). Fibre numbers were estimated from cross-sectional slices of whole muscle, obtained at autopsy following sudden, accidental death. This percentage decrease is similar to the change in strength found between these age groups in the present study. Lexell et al. (1983) did not find a significant difference in fibre size between the two age groups, but other authors have reported that Type II muscle fibres had smaller cross-sectional areas in old subjects (see Larsson, 1982 for review). This point remains controversial in the case of Type I fibres - only Larsson et al. (1979) have observed a decrease in their cross-sectional area in older subjects. In other investigations Type I size was

unchanged or even increased (Tamonaga, 1977; Aniansson et al., 1981; Clarkson et al., 1981; Grimby et al., 1982).

A decrease in muscle fibre number with age has also been demonstrated in rodent hindlimb muscles (Rowe, 1979; Tauchi et al., 1971; Gutmann and Hanzlikova, 1972; Hooper, 1981). Some authors have reported increased fibre cross-sectional areas in old animals (Rowe, 1969; Hooper, 1981). In rats, Silbermann et al. (1983) observed this increase for Type I fibres only.

The relative proportion of Type I muscle fibres may thus increase in some muscles of old subjects, due to a preferential atrophy or loss of the Type II fibre complement, and a compensatory hypertrophy of the Type I fibres (Campbell et al., 1973; Larsson, 1982). It has been suggested that Type I muscle fibres have a lower capacity for isometric force development per cross-sectional area than Type II fibres, based on observations of the strength of individuals with different compositions of muscle fibre types (Komi and Karlsson, 1978; Larsson et al., 1979; Young, 1984). Burke (1981) has also provided evidence that Type I fibres produce less specific tension, by analysis of individual motor unit properties in various leg muscles of cats. Some controversy exists on this point (e.g. Hulten et al., 1975; Maughan et al., 1983), but if Type I fibres are a relative handicap for isometric force production, then old people may be at a disadvantage.

This disadvantage of Type I fibre predominance might be expected to be more pronounced in dynamic strength tests which require concentric contraction with rapid force development by the muscle fibres (Thorstensson et al., 1976; Coyle et al., 1979; Vandervoort et al., 1984). However, such an effect was not obvious in Larsson et

al.'s (1979) data, which involved both isometric and dynamic strength measurement. This hypothesis should perhaps be specifically tested in an investigation which includes older subjects than the 60 to 69 yr old men examined by Larsson and co-workers.

Greater total change with increased age was present in absolute plantarflexor muscle strength than dorsiflexor muscle strength. These muscles are an important part of the anti-gravity extensor group. Hence, the ability to control rotation at the ankle joint is impaired with aging and the problem could be particularly important following a period of disuse leading to muscle atrophy. In healthy young adults, the plantarflexor muscles work at relatively low percentages of maximum capacity during moderate activities like walking, but in the elderly the reserve or safety margin is reduced.

C. Speed of Muscle Contraction in the Elderly

As mentioned, both dorsiflexor and plantarflexor twitch times increased in the older age groups. Similar observations were made for male plantarflexor muscles in the study of Davies et al. (1983). McDonagh et al. (1984) noted a trend to increased twitch times in the elbow flexor muscles of old vs young men that failed to reach statistical significance. Twitch times for the plantarflexor muscles were longer in the present study for both young and old subjects, as compared to corresponding measurements in the laboratory of Davies and co-workers. This could be due to differences in the apparatus for recording tension and in the method of measuring twitch times.

However, the size of the change in twitch times with aging is similar in the two studies from different laboratories. Some possible explanations for the prolongation of the twitch are discussed below.

(1) First hypothesis: change in elastic properties of tendons. The amount of elasticity in a muscle's tendon will affect the time-course of its twitch, and a possible hypothesis is that twitch prolongation occured with aging because tendon elasticity had increased, thereby slowing the rate of tension development (Carlson and Wilkie, 1974). But, as discussed in the section "Peak tension of the isometric twitch", elasticity may have actually been decreased in the elderly muscles. Possibly because of the reduced excitable muscle mass in older people, absolute passive tensions created in the dorsiflexor and plantarflexor muscle-tendon complexes, by stretching them to their respective isometric test positions, were not systematically different between young and old adults. This result was somewhat unexpected as Botelho et al. (1954) and Campbell et al. (1973) had found greater resistance to stretch in elderly thumb and great toe joints, respectively. There may be a difference between these digital joints and the ankle in their response to aging that warrants further study. It also possible that stretching or loosening up of the connective tissue bonds took place during the testing procedures in the present investigation (Kottke et al., 1966). An alternative testing procedure would be to measure passive tension using small sinusoidal oscillations of the joint in the manner of Walsh (e.g. Lakie et al., 1980).

(2) Second hypothesis: conversion to slower myosin ATPase in muscle fibres.

(3) Third hypothesis: preferential decrease in number and/or size of Type II motor units.

The end result of either conversion to a slower myosin ATPase in the same muscle fibres or of a preferential decrease in the Type II motor unit complement would be to produce a muscle with a longer twitch. It is difficult to separate the relative contributions of these two factors (Campbell et al., 1973). Whatever the cause, it has been reported that the proportion of Type I muscle fibres does increase with aging, based on several studies of human and animal tissue (see above and Larsson, 1982).

It might be expected that the greatest changes would be observed in muscles that have the highest initial complement of Type II fibres. Changes with aging in twitch times of the gastrocnemius muscle, reported to have approximately equal proportions of Type II and Type I fibres in young adults, were compared to changes in the soleus muscle, which is predominately Type I in composition (see Vandervoort and McComas (1983) for a discussion of research on these two muscles). Mean soleus muscle contraction times were found to be similar in young and old adults but gastrocnemius muscles had significantly longer twitches. A greater effect of age was also observed in the twitch of the entire plantarflexor group than in the soleus alone. Unfortunately, no reports of comparisons between the fibre composition of young and old soleus and gastrocnemius muscles were found in the literature.

An increased muscle activity pattern appears to prolong twitch

times in young adults; Sale et al. (1983) observed longer twitches of the triceps surae muscle group in weight-trainers as compared to controls. And disuse resulted in a faster twitch contraction time for this muscle group in a study of young men whose leg had been immobilized (Davies and White, 1983a). The same finding was reported for immobilized young rat soleus muscles (Witzmann et al., 1982). It is not known if this effect would also occur in old muscle that was immobilized. In the present study contraction times were increased in the elderly, the opposite effect to the immobilization response. This may be another indication of the fairly active lifestyles adopted by the sample of old people tested - evidence of disuse was not present in the twitch times. The aging process is clearly more complex than a simple reflection of increasing inactivity.

An advantage of a prolonged twitch time-course is that the muscle will produce a relatively greater proportion of its total tension-generating capacity at a given submaximal frequency of stimulation. In addition, it will exhibit maximum fused tetanic tension at a relatively lower rate of firing. Davies and White (1983) have reported this to be the case in comparisons of young and old human triceps surae muscles. Consequently, old people should be more efficient, in the sense that fewer nerve impulses are needed to drive their muscle contractions. It would be of interest to compare firing frequencies of young and old muscles during sustained voluntary contractions. The intramuscular recording technique of Bigland-Ritchie and co-workers could be used to monitor motor unit activity (e.g. Bellemare et al., 1983).

(4) Fourth hypothesis: change in Ca^{2+} regulatory system (and hence change in active state duration). The actual time in which Ca^{2+} is bound to troponin following a twitch stimulus, thereby releasing the inhibitory influence of troponin on actin-myosin interactions, may be prolonged in aged muscle (this period of tension generation by the myofilaments has been designated by Hill (1949) as the "active state" duration). Hence, a fourth factor which could alter twitch times is a change in the regulation of free Ca^{2+} levels in the myoplasm. Obtaining such information will require the use of techniques like electron microscopy to quantify the volume of the terminal cisternae in the sarcoplasmic reticulum (cf. Kugelberg and Thornell, 1983). Presently, there are just scant reports of changes in sarcoplasmic reticulum of old human muscle (Tomonaga, 1977; Shafiq et al., 1978). Aged rats have been shown to have decreased sarcoplasmic reticulum volumes in the gastrocnemius muscle (DeCoster et al., 1981), but aged mice had little change in this structure (Ludatscher et al., 1983). Ludatscher et al. (1983) also found enforced endurance running caused formation of tubular aggregates in the old mouse gastrocnemius muscles, an effect which was not seen in young exercised mice. Differences in the housing conditions of animals, differences in opportunity for exercise, interspecies differences and even variation among strains of a given species can lead to opposing conclusions from research using animal models.

As hypothyroidism has been shown to slow muscle contraction (Lambert et al., 1951; Takamori et al., 1971), a speculative hypothesis would be that the elderly population tested may have had subclinical levels of this disease. However, the prevalence of overt

hypothyroidism, including untreated cases, has been found to be only 1 to 2% in elderly community-dwellers (see Campbell et al., 1981). None of the subjects in the present study reported taking thyroid medication. A further argument against this hypothesis is the observation that some increase in twitch times was also noted in the middle-aged adults, as compared to 20 to 30 yr olds. Prolongation of twitch times may thus be due, at least in part, to normal genetic regulation of the developmental/maturation/aging sequence in human neuromuscular function. It is of interest that Robbins and co-workers (Kelly and Robbins, 1983) have observed changes in transmission across mouse neuromuscular junctions beginning at middle-age for the life-span of the strain of mice tested.

D. Potentiation of the Isometric Twitch Following MVC

The isometric twitches of both the dorsiflexor muscles and the plantarflexor muscles were clearly changed in all age groups following a 5s MVC; peak twitch torque was increased and twitch times were shortened. As had been reported before, when twitch torques were normalized with respect to resting values, potentiation of peak twitch torque was greater in the dorsiflexor muscles than the plantarflexor muscles (Belanger et al., 1983; Vandervoort et al., 1983). This trend held for all age groups except the middle-aged category. The reason for the unique pattern in middle-aged adults was not clear, but the ratios of plantarflexor to dorsiflexor MVC were particularly high in this group. An overall trend of decreased potentiation with increasing age was observed and it may be that at middle-age the dorsiflexor

muscles have been more affected than the plantarflexor muscles with regard to capacity for potentiation.

The basis of potentiation is not clearly understood, although altered kinetics of muscle-activating Ca^{2+} is a likely mechanism (Burke, 1981). The phenomenon seems to be specific to certain muscles; Vandervoort and McComas (1983) did not observe potentiation in young adult human soleus muscles following tetanic stimulation, but it was present in the lateral gastrocnemius muscles of the same subjects. Perhaps the elderly gastrocnemius muscles were also mainly responsible for altered properties of the potentiated plantarflexor twitches. The longer twitches of the elderly were more susceptible to the speeding up aspect of potentiation which produces not only a larger twitch tension but also a shorter twitch. A speculative hypothesis about the mechanism for this effect of aging is that the amount of calcium released by the sarcoplasmic reticulum following the MVC was relatively diminished, as compared to young adults, thereby producing less potentiation and a faster contraction/relaxation cycle. One functional implication of potentiation is that the muscle can be put in a state of readiness for contraction by a brief period of MVC prior to an intended movement (Belanger et al., 1983; Vandervoort et al., 1983).

E. Flexibility of the Ankle Joint

The limit to which the ankle could be dorsiflexed was reduced in the older age groups, although the effect was not pronounced. Even the 80 to 100 yr old ankle could be rotated into a position of 31 ^{o} of dorsiflexion, on average, for males; the corresponding value for females was 27 ^{o}. An overall trend can be seen in the data for a

greater loss of flexibility in women and this has been observed before (Bell and Hoshizaki, 1981; Flatten and Rice, 1982).

It is not clear from the present study why the limit of dorsiflexion decreased in the old subjects. The total stiffness of the elastic tissue, as measured at 10^{o} of dorsiflexion, did not increase with aging, although passive tension was greater, if expressed relative to excitable muscle mass. It was not possible in the present study to determine whether it was the extent of elongation of the muscle belly or the extent of elongation of the tendon which limited joint rotation. However, Halar et al. (1978) have shown that movement of the human ankle joint in dorsiflexion is permitted primarily by changes in the length of the muscle, and that the Achilles tendon is relatively inextensible. Hooper (1981) reported shorter fibre lengths in hindlimb muscles of old mice, due to a loss of sarcomeres with aging. Such a change would limit joint range of motion if it occurred in human muscles, but the author is unaware of any studies in this regard. It is also possible that degenerative processes had caused bony limitations to ankle joint range of motion in older subjects. In a future study, it would be useful to compare passive tensions developed at the limit of movement of individual ankles, to determine if there is a critical, stopping force in the passive length-tension curve which old people reach sooner when the ankle is rotated.

It is beneficial to the elderly to have an adequate ankle joint range of motion if a normal gait pattern is to be maintained. Considerable flexibility was found in the ankles of this sample of the healthy elderly. Judging from the data of Bell and Hoshizaki (1981), the ankle may be one of the least affected joints by aging, and this

might be due to its extensive use in the healthy, mobile person. There is evidence that daily stretching can improve range of motion in the elderly (Munns, 1981), although it is not known whether such a program could completely prevent flexibility loss in the aged joint.

V. SUMMARY AND CONCLUSIONS

This investigation has involved observations on the maximal voluntary strength and isometric twitch of the ankle dorsiflexor and plantarflexor muscle groups in a sample of 111 healthy men and women aged from 20 to 100 yr. Additional comparisons of twitch times of the individual muscles in the triceps surae group, and measurements of their cross-sectional areas, were made in selected groups of young and very old men and women. Summary statements regarding the effects of aging on the human neuromuscular system are as follows:

1. Reliable assessment of neuromuscular function can be made in old adults using measurements of maximal strength and electrophysiological techniques.

2. Maximum voluntary isometric strength of the ankle dorsiflexors and plantarflexors was lower in old adults than in young adults. Men were stronger than women at all ages. The trend observed in the data was for a decrease in strength following the fifth decade of life. The absolute loss of strength was much greater for the plantarflexor muscle group than the dorsiflexor group; the relative loss was similar.

3. The majority of men and women at all ages were able to utilize their descending motor pathways for optimal muscle activation, so that an interpolated stimulus of the motor nerve produced no additional tension. Some subjects needed several practice attempts to achieve this goal.

4. A decreased excitable muscle mass was the apparent explanation for the lower strength of the elderly.

5. Isometric twitch times were prolonged and the rate of tension development was reduced in the elderly for both dorsiflexor and

plantarflexor muscle groups. An additional observation was that the soleus muscle showed less change than the gastrocnemius muscle.

6. Capacity for post-activation potentiation of the twitch was present, but reduced in the older age groups.

7. The passive tension induced in the dorsiflexor muscles and plantarflexor muscles by 20° of ankle rotation was similar for all age groups.

8. The limit of dorsiflexion to which the ankle could be rotated was reduced as age increased. Considerable movement of the ankle was still possible in the oldest subjects.

Original observations in this study regarding the effects of aging on human neuromuscular function were made by:

(i) comparing the opposing muscles of the ankle joint.

(ii) extending the number and age range of very old subjects tested beyond that of previous work which measured voluntary strength, twitch time and passive tension of these muscles.

(iii) using the interpolated twitch procedure to demonstrate that the elderly could generally achieve full motor unit activation.

(iv) examining the capacity for post-activation potentiation in aged muscle.

(v) implementing an ultrasound imaging technique to obtain cross-sectional areas of the soleus and gastrocnemius muscles.

(vi) implementing a sub-maximal stimulation technique to compare twitch times of the gastrocnemius and soleus muscles.

Several areas of future research have been noted in the discussion of the results. These are summarized below in the form of research questions:

<u>With regard to exercise training programs for the elderly</u>:

Can maximal voluntary strength of the ankle joint muscles be increased by a program of high-resistance exercise training?

With regard to muscle fibre composition in the aged dorsiflexor and plantarflexor muscles:

1. Is there a decrease in the total number of muscle fibres with aging and what is the extent of fat and connective tissue replacement of muscle in the aged limb?

2. Are there differences between young and old muscle in myosin ATPase characteristics or in the Ca^{2+} regulatory system?

With regard to neuromuscular function:

1. Are the elderly at a greater disadvantage for rapid, concentric force production than for isometric tension development because of their slower rate of muscle contraction?

2. Are the more slowly contracting, weaker muscles of the elderly a contributing factor to the geriatric problem of falling?

It should be stressed that this investigation dealt with questions about aging of the healthy population. Loss of muscle strength in the disabled elderly is also an important topic for research. The effects of prolonged immobilization on the elderly neuromuscular system have not been documented; nor have the expected benefits of aggressive rehabilitation.

In summary, insight has been gained into the differences in neuromuscular function between age groups of healthy men and women spanning the range of 20 to 100 yr. It is anticipated that this information, besides enhancing knowledge about the aging process, will be applied to several situations: in the practice of clinical assessment and rehabilitation of people of different ages, in the planning of exercise programs for the elderly and finally, in the formulation of new research questions.

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APPENDIX A

CONSENT FORM (NORMAL SUBJECTS)

I have been asked by Dr./Mr. _____ if I would consent to a research study being performed on myself/ _____. I have been told the purpose of the study is to study some of the changes which take place in aging muscle. I understand that the study involves the delivery of weak electric shocks through a pair of electrodes on the skin. I have been told that although the study is not of any medical benefit, it is not harmful, carries no risk and is similar to investigations carried out on patients for diagnostic purposes. I further understand that I have the right to withdraw myself/my ward from the study at any time.

Bearing these factors in mind, I hereby give permission for the above study to be performed on myself/_____.

_____ Guardian _____ Date

_____ Doctor _____ Date

_____ Witness _____ Date

I, _____ have received the sum of $ _____ in payment for my participation in the above project.

DATE: _____ SIGNED _____

Table A1. Individual Data for Height, Weight, Passive Tension at 30°P and 10°D (PT30D, PT10D), and Passive Range of Ankle Joint Movement in Dorsiflexion (ROM-DF)

Subject (#)	(Init)	Sex	Age (Yr)	Height (cm)	Weight (kg)	PT30P (N.m)	PT10D (N.m)	ROM-DF (degree)
001	AM	F	70	160	61.2	2.2	3.6	22
002	CM	M	80	175	74.4	3.1	2.9	25
003	BM	M	78	174	71.5	2.0	0.7	22
004	HM	M	73	194	74.2	2.5	4.8	25
005	MM	F	66	173	72.4	1.7	5.0	28
006	HG	M	82	164	57.8	1.3	2.2	35
007	RP	M	80	171	72.8	2.4	3.6	30
008	SW	M	75	165	66.0	2.7	3.6	22
009	MD	F	78	156	38.9	0.8	2.9	25
010	AP	M	82	166	65.6	2.0	3.6	27
011	DL	F	82	155	49.3	1.5	3.0	25
012	EC	F	71	158	67.7	1.8	3.7	24
013	DM	F	67	155	60.5	1.7	1.8	35
014	RL	M	70	166	63.0	2.0	3.2	30
015	HF	M	82	168	66.4	1.3	2.2	33
016	DK	F	69	157	57.3	1.3	2.9	18
017	AP	M	73	173	68.3	2.4	3.6	30
018	VW	F	66	156	59.0	2.0	2.5	30
019	JG	M	68	164	76.3	2.0	1.1	38
020	JW	M	73	158	60.1	1.3	4.0	25
021	ME	F	72	169	65.7	2.0	2.5	23
022	CE	M	73	171	67.2	1.7	3.6	22
023	JR	M	75	185	94.0	3.8	3.2	26
024	MM	M	60	175	79.4	2.7	4.0	21
025	KD	M	73	180	71.8	1.3	2.2	36
026	JO	M	71	171	78.4	1.7	2.9	30
027	SP	M	67	174	72.4	2.0	3.2	30
028	JH	M	61	176	94.7	3.4	7.5	20
029	BW	M	77	181	61.5	0.6	1.8	40
030	MC	F	62	156	54.6	1.3	1.8	40
031	JC	M	68	180	78.5	4.2	7.9	20
032	MW	F	62	173	62.0	2.0	2.2	28
033	DM	M	62	164	62.0	1.7	3.6	30
034	MR	F	76	167	68.8	1.7	4.0	25
035	MH	F	77	156	48.2	1.7	1.8	35
036	RE	M	61	175	60.7	2.0	2.2	35
037	LS	M	65	168	68.4	2.0	1.8	25
038	AS	F	63	155	50.6	0.9	1.8	40
039	TL	F	70	170	62.0	1.5	1.8	23
040	RC	M	69	172	62.4	1.7	2.5	31
041	MV	F	63	158	55.9	1.6	3.9	25
042	BM	M	74	166	64.9	1.7	2.9	30
043	NN	F	87	161	63.8	1.0	3.2	26

Table A1 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	Height (cm)	Weight (kg)	PT30P (N.m)	PT10D (N.m)	ROM-DF (degree)
044	WS	F	75	165	54.3	1.3	3.6	30
045	BL	M	69	165	57.6	1.3	2.9	37
046	HL	M	85	162	63.2	1.7	1.4	38
047	RP	F	91	157	42.4	1.3	3.2	25
048	BC	M	75	182	87.8	2.4	2.5	40
049	DE	M	82	170	78.2	2.7	6.1	30
050	AS	F	98	155	51.4	1.7	4.7	20
051	MM	M	74	180	68.5	2.2	1.5	38
052	FB	M	100	165	63.5	2.7	2.5	30
053	RL	M	71	183	78.8	1.7	2.2	40
054	BS	M	94	167	58.4	2.2	1.1	31
055	LS	F	79	161	62.8	1.7	2.2	38
056	JC	F	82	164	63.2	2.0	2.9	30
057	CD	M	69	171	92.8	4.1	3.6	30
058	LD	F	62	163	75.6	1.8	2.9	31
059	NS	F	82	151	61.2	1.3	1.8	33
060	GB	M	90	170	68.7	2.4	2.5	39
061	AM	F	69	151	56.7	3.4	2.5	29
062	GL	M	79	166	67.8	1.8	1.8	37
063	AM	M	92	170	70.0	2.4	3.6	30
064	AH	M	87	163	65.6	3.8	2.9	22
065	BW	M	69	178	84.4	2.4	3.2	31
066	MM	M	61	179	69.3	2.0	1.5	40
067	SF	F	23	170	58.3	1.6	3.6	31
068	KR	F	31	164	53.2	0.9	2.0	40
069	NG	F	24	164	59.0	1.3	1.1	40
070	JG	F	30	162	67.0	1.6	2.9	40
071	AV	F	20	165	56.3	1.3	1.4	40
072	TC	F	29	161	60.3	1.5	2.2	40
073	ET	F	31	158	53.5	1.8	2.2	40
074	TB	M	27	183	82.2	2.4	2.0	40
075	PV	F	27	158	50.8	2.0	2.9	38
076	SM	M	23	173	80.0	2.0	3.2	40
077	JB	M	25	185	75.0	2.0	2.9	35
078	KM	F	29	155	50.7	1.3	1.4	40
079	TB	M	26	173	64.9	1.3	2.0	38
080	JM	M	27	173	70.3	1.8	2.9	40
081	MC	M	23	182	76.0	3.4	2.5	32
082	BL	F	30	156	45.7	0.9	1.8	35
083	JJ	M	30	165	79.8	2.4	3.6	33
084	SN	F	26	148	45.0	1.3	2.2	31
085	JS	M	31	173	60.3	2.0	2.2	40
086	CD	M	28	180	76.9	4.1	4.7	22
087	MH	M	27	186	79.5	2.4	4.7	31
088	PC	M	28	173	63.6	0.0	0.0	0
089	KB	F	22	157	53.0	0.0	0.0	0
090	NK	F	29	165	54.0	0.0	0.0	0
091	JB	M	32	183	77.0	0.0	0.0	0
092	JK	M	29	180	70.0	0.0	0.0	0

Table A1 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	Height (cm)	Weight (kg)	PT30P (N.m)	PT10D (N.m)	ROM-DF (degree)
093	TV	M	28	165	56.0	0.9	2.9	40
094	DB	M	45	179	59.4	2.4	3.9	30
095	RM	M	45	184	82.8	1.3	2.0	35
096	PY	F	41	169	70.0	0.8	1.1	40
097	BV	M	40	181	91.6	1.4	4.1	30
098	CC	M	44	183	99.9	3.3	4.5	30
099	BC	F	40	159	65.6	0.9	1.2	40
100	JD	M	45	174	80.1	1.2	2.2	40
101	MM	M	40	178	75.5	2.0	3.6	30
102	EG	F	49	174	67.7	1.7	2.9	40
103	AP	F	43	156	56.3	1.3	3.9	30
104	EK	M	44	170	69.7	0.9	2.5	40
105	DP	M	43	167	70.6	2.2	5.0	28
106	HL	F	42	159	79.5	0.8	2.2	36
107	SK	F	47	168	75.2	2.0	4.3	28
108	JB	F	41	166	72.5	1.3	2.2	33
109	GH	M	42	171	64.0	1.7	2.9	30
110	AM	M	49	181	81.7	1.5	2.9	36
111	MM	F	44	157	46.8	1.3	3.4	30
112	LC	F	41	166	71.6	1.7	3.2	30
113	DN	F	52	155	54.5	0.9	1.6	40
114	MM	F	100	144	46.0	0.9	1.8	28
115	HN	M	98	165	64.2	1.7	2.2	30
116	MH	F	87	156	51.0	0.9	2.0	28

Table A2. Individual Data for Resting and Potentiated Isometric Dorsiflexor Twitches. Variables are Compound Muscle Action Potential (M-wave), Contraction Time (CT), One-Half Relaxation Time (1/2RT) and Peak Twitch Torque (P_t)

				RESTING				POTENTIATED			
Subject (#)	(Init)	Sex	Age (Yr)	M-wave (Mv)	CT (ms)	1/2RT (ms)	P_t (N.m)	M-wave (Mv)	CT (ms)	1/2RT (ms)	P_t (N.m)
001	AM	F	70	9.4	100	80	1.7	10.0	70	65	2.9
002	CM	M	80	5.8	130	115	4.0	6.0	115	80	4.6
003	BM	M	78	9.0	115	150	4.7	9.0	105	95	7.5
004	HM	M	73	7.5	125	125	5.4	7.5	110	90	6.1
005	MM	F	66	8.4	125	125	3.7	8.8	110	80	4.6
006	HG	M	82	4.0	90	85	2.4	3.6	85	70	4.0
007	RP	M	80	6.8	125	130	3.5	6.8	105	95	4.7
008	SW	M	75	11.0	105	90	4.7	11.3	95	70	7.2
009	MD	F	78	5.6	100	90	1.7	6.2	105	90	2.0
010	AP	M	82	6.4	120	120	3.2	6.4	120	85	4.3
011	DL	F	82	4.5	115	100	2.2	4.8	100	70	3.6
012	EC	F	71	5.0	105	115	1.3	5.6	85	70	1.4
013	DM	F	67	4.8	130	120	3.9	5.0	115	85	6.0
014	RL	M	70	11.0	110	90	2.7	12.0	110	60	4.4
015	HF	M	82	4.3	95	80	2.8	4.8	100	70	4.9
016	DK	F	69	3.4	115	130	2.0	3.4	115	90	2.3
017	AP	M	73	7.4	120	145	2.7	7.4	115	135	2.6
018	VW	F	66	8.0	110	80	1.2	8.4	85	65	2.1
019	JG	M	68	7.8	90	105	4.3	6.0	105	110	4.7
020	JW	M	73	15.5	80	70	2.0	15.5	75	45	3.2
021	ME	F	72	1.7	125	135	1.4	1.7	120	95	1.4
022	CE	M	73	3.2	95	125	1.9	2.8	90	75	2.4
023	JR	M	75	7.4	120	110	4.9	7.5	110	70	5.7
024	MM	M	60	11.0	100	105	4.2	11.5	90	55	4.9
025	KD	M	73	4.6	125	135	3.7	5.0	115	110	5.0
026	JO	M	71	9.0	110	120	3.4	9.0	105	80	5.4
027	SP	M	67	6.6	100	95	2.1	7.0	90	60	4.2
028	JH	M	61	6.4	90	90	4.2	6.4	90	60	5.7
029	BW	M	77	5.8	110	125	4.0	5.8	110	110	4.4
030	MC	F	62	12.0	115	110	3.4	12.5	105	80	4.3
031	JC	M	68	6.0	110	105	2.9	6.1	110	90	4.3
032	MW	F	62	4.5	100	140	2.4	4.5	110	110	3.3
033	DM	M	62	6.7	90	90	2.0	6.2	90	75	2.8
034	MR	F	76	4.3	110	165	1.1	4.5	105	80	1.8
035	MH	F	77	9.5	100	95	1.6	9.5	100	70	2.2
036	RE	M	61	10.0	100	75	6.4	10.0	100	75	9.7
037	LS	M	65	6.6	105	140	2.2	6.8	85	95	2.3
038	AS	F	63	15.0	115	120	2.9	15.0	105	75	3.4
039	TL	F	70	4.0	115	145	2.9	4.4	110	115	3.4
040	RC	M	69	5.2	110	125	2.2	5.2	105	110	2.7
041	MV	F	63	6.5	110	130	4.2	6.2	105	85	4.7

Table A2 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	RESTING M-wave (Mv)	CT (ms)	1/2RT (ms)	P_t (N.m)	POTENTIATED M-wave (Mv)	CT (ms)	1/2RT (ms)	P_t (N.m)
042	BM	M	74	3.4	120	140	1.7	3.4	130	120	2.4
043	NN	F	87	2.8	130	190	1.0	2.8	115	145	1.4
044	WS	F	75	8.0	100	110	1.0	8.0	110	80	1.9
045	BL	M	69	8.2	100	70	4.4	8.4	100	55	4.9
046	HL	M	85	5.4	100	75	2.1	5.4	100	70	2.4
047	RP	F	91	8.0	120	100	2.9	8.1	110	85	3.4
048	BC	M	75	8.4	125	140	4.6	8.6	120	110	6.4
049	DE	M	82	6.2	120	160	3.2	6.4	125	115	3.9
050	AS	F	98	3.2	135	150	1.7	3.2	155	145	1.4
051	MM	M	74	6.0	150	130	1.4	6.0	120	140	1.6
052	FB	M	100	3.6	135	125	2.8	3.6	127	103	3.7
053	RL	M	71	6.6	115	110	2.9	3.4	115	90	3.2
054	BS	M	94	5.8	135	140	2.3	5.8	125	130	3.0
055	LS	F	79	9.2	135	135	3.7	10.0	120	110	4.1
056	JC	F	82	4.7	120	115	1.7	4.8	115	120	2.6
057	CD	M	69	6.4	125	115	3.0	6.6	130	90	4.3
058	LD	F	62	4.0	125	120	1.9	4.8	115	100	2.9
059	NS	F	82	4.8	120	130	1.1	4.9	135	110	1.4
060	GB	M	90	5.4	125	110	1.7	5.4	120	105	2.4
061	AM	F	69	12.0	105	120	2.6	11.0	100	80	3.4
062	GL	M	79	9.0	120	140	2.4	9.0	115	120	2.4
063	AM	M	92	5.8	150	160	2.4	5.8	155	180	2.4
064	AH	M	87	2.2	150	175	0.9	2.5	150	125	1.0
065	BW	M	69	3.6	120	105	2.9	4.8	135	90	5.1
066	MM	M	61	6.4	110	100	1.7	6.1	120	95	3.2
067	SF	F	23	10.5	90	85	1.4	10.5	90	65	3.6
068	KR	F	31	10.5	90	80	2.1	11.0	90	65	5.0
069	NG	F	24	6.0	100	75	4.9	6.0	90	70	7.3
070	JG	F	30	12.0	100	85	2.7	12.0	95	70	3.3
071	AV	F	20	7.0	90	100	2.1	7.2	90	70	4.1
072	TC	F	29	5.4	100	95	3.0	5.3	100	70	5.3
073	ET	F	31	8.8	100	80	1.6	9.0	95	70	2.6
074	TB	M	27	6.8	110	105	5.4	7.4	105	80	7.7
075	PV	F	27	13.5	100	80	5.0	14.3	95	65	7.2
076	SM	M	23	10.1	90	70	4.0	10.4	90	65	8.3
077	JB	M	25	5.0	110	80	2.6	5.1	105	70	3.9
078	KM	F	29	10.5	105	105	2.6	11.0	100	75	4.9
079	TB	M	26	10.3	110	75	5.1	10.0	105	60	7.7
080	JM	M	27	7.4	90	85	2.3	7.8	90	65	4.3
081	MC	M	23	9.4	95	70	4.7	10.0	90	65	9.5
082	BL	F	30	6.3	105	75	2.4	6.3	95	65	2.6
083	JJ	M	30	15.0	105	90	4.7	15.5	105	70	7.7
084	SN	F	26	9.6	80	60	1.3	10.6	80	55	2.4
085	JS	M	31	9.8	100	90	3.4	10.0	105	75	5.7
086	CD	M	28	8.4	100	80	6.9	9.0	100	70	11.4

Table A2 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	RESTING M-wave (Mv)	CT (ms)	1/2RT (ms)	P_t (N.m)	POTENTIATED M-wave (Mv)	CT (ms)	1/2RT (ms)	P_t (N.m)
087	MH	M	27	10.6	100	80	4.6	10.8	95	60	7.5
088	PC	M	28	0.0	0	0	0.0	0.0	0	0	0.0
089	KB	F	22	0.0	0	0	0.0	0.0	0	0	0.0
090	NK	F	29	0.0	0	0	0.0	0.0	0	0	0.0
091	JB	M	32	0.0	0	0	0.0	0.0	0	0	0.0
092	JK	M	29	0.0	0	0	0.0	0.0	0	0	0.0
093	TV	M	28	10.5	100	95	2.1	12.5	95	65	3.7
094	DB	M	45	9.2	130	120	4.0	8.8	125	95	4.3
095	RM	M	45	9.4	115	100	2.0	9.6	110	90	2.9
096	PY	F	41	9.2	115	110	2.4	9.2	110	90	5.2
097	BV	M	40	6.8	105	90	4.3	6.8	115	75	6.5
098	CC	M	44	8.6	135	115	4.8	10.0	120	90	7.6
099	BC	F	40	7.2	140	145	3.9	7.4	130	130	3.8
100	JD	M	45	8.9	110	95	5.5	8.4	105	90	8.4
101	MM	M	40	10.6	100	85	3.3	10.9	90	65	5.2
102	EG	F	49	9.4	105	115	2.5	9.4	110	105	3.9
103	AP	F	43	10.0	105	90	3.1	10.5	110	75	4.6
104	EK	M	44	11.0	100	90	5.2	13.0	95	65	7.7
105	DP	M	43	11.0	95	90	4.0	10.0	95	65	5.9
106	HL	F	42	10.5	105	100	5.2	11.0	100	75	6.7
107	SK	F	47	15.0	110	75	4.2	15.0	105	75	5.7
108	JB	F	41	9.2	110	110	3.6	9.4	100	95	5.0
094	GH	M	42	9.4	100	85	5.3	9.6	100	75	7.6
110	AM	M	49	12.0	115	125	6.2	12.0	105	100	8.6
111	MM	F	44	13.0	110	110	3.2	13.0	105	80	4.6
112	LC	F	41	9.2	115	120	4.7	9.2	115	115	6.4
113	DN	F	52	12.0	110	120	4.1	12.5	100	95	6.6
114	MM	F	100	5.5	140	130	0.7	5.5	160	150	0.6
115	HN	M	98	8.8	155	150	1.9	8.8	130	125	2.4
116	MH	F	87	8.4	140	130	2.4	8.8	140	110	3.7

Table A3. Individual Data for Resting and Potentiated Isometric Plantarflexor Twitches. Variables are Compound Muscle Action Potential (M-wave), Contraction Time (CT), One-half Relaxation Time (1/2RT) and Peak Twitch Torque (P_t)

Subject (#)	(Init)	Sex	Age (Yr)	RESTING M-wave (Mv)	RESTING CT (ms)	RESTING 1/2RT (ms)	RESTING P_t (N.m)	POTENTIATED M-wave (Mv)	POTENTIATED CT (ms)	POTENTIATED 1/2RT (ms)	POTENTIATED P_t (N.m)
001	AM	F	70	12.0	150	120	11.2	13.0	150	100	14.0
002	CM	M	80	10.5	175	135	16.0	13.0	125	125	23.6
003	BM	M	78	11.5	200	210	15.2	14.5	145	180	17.9
004	HM	M	73	6.4	165	125	22.9	6.9	145	115	22.9
005	MM	F	66	8.8	190	120	14.3	7.6	160	100	14.3
006	HG	M	82	15.5	170	125	12.3	15.5	155	95	12.3
007	RP	M	80	12.0	215	135	11.3	12.5	195	120	11.6
008	SW	M	75	19.5	160	150	12.9	20.0	140	120	15.4
009	MD	F	78	13.5	160	125	12.5	10.5	145	105	12.5
010	AP	M	82	12.5	170	145	13.2	12.0	145	105	15.7
011	DL	F	82	7.8	185	135	12.5	8.4	150	105	14.3
012	EC	F	71	8.6	180	195	15.7	9.0	175	173	17.3
013	DM	F	67	10.5	175	125	9.7	11.0	155	115	10.0
014	RL	M	70	15.3	145	110	11.8	14.5	135	95	11.8
015	HF	M	82	4.4	185	170	10.0	4.4	150	160	9.7
016	DK	F	69	11.5	185	145	13.2	12.0	145	105	16.8
017	AP	M	73	14.5	215	190	16.4	14.5	170	165	15.4
018	VW	F	66	7.5	175	150	15.4	6.5	140	130	20.7
019	JG	M	68	11.0	160	115	12.9	13.0	125	95	19.0
020	JW	M	73	13.8	160	120	13.9	17.5	140	105	21.3
021	ME	F	72	8.0	210	130	11.1	8.0	180	111	8.0
022	CE	M	73	10.5	185	140	11.3	10.0	160	110	14.3
023	JR	M	75	8.0	175	130	14.8	8.0	145	105	17.5
024	MM	M	60	20.5	165	100	12.2	23.5	145	70	16.8
025	KD	M	73	16.0	180	115	17.2	15.0	125	100	21.8
026	JO	M	71	14.0	160	100	15.6	16.3	145	90	18.2
027	SP	M	67	10.5	160	125	9.5	11.3	125	105	13.2
028	JH	M	61	13.5	160	120	23.6	10.5	140	100	23.6
029	BW	M	77	14.0	190	115	11.1	12.8	160	115	11.1
030	MC	F	62	8.5	175	145	10.0	12.0	140	130	12.9
031	JC	M	68	8.0	190	125	13.2	6.5	170	100	15.0
032	MW	F	62	14.0	195	130	17.9	14.3	170	110	21.5
033	DM	M	62	9.5	155	105	15.2	10.0	125	110	20.4
034	MR	F	76	10.5	195	175	11.3	11.0	165	130	12.5
035	MH	F	77	7.4	160	125	8.9	8.0	140	105	12.9
036	RE	M	61	9.5	175	95	10.0	8.5	175	80	10.7
037	LS	M	65	19.0	160	110	10.7	19.0	135	90	16.1
038	AS	F	63	21.0	180	120	8.2	21.5	150	95	9.1
039	TL	F	70	6.4	210	150	18.6	6.4	170	130	19.3
040	RC	M	69	13.0	200	145	12.2	13.0	195	135	12.9
041	MV	F	63	3.8	170	110	9.1	3.7	155	95	8.6

Table A3 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	RESTING M-wave (Mv)	RESTING CT (ms)	RESTING 1/2RT (ms)	RESTING P_t (N.m)	POTENTIATED M-wave (Mv)	POTENTIATED CT (ms)	POTENTIATED 1/2RT (ms)	POTENTIATED P_t (N.m)
042	BM	M	74	7.0	175	155	10.0	7.0	160	130	11.8
043	NN	F	87	3.2	205	210	10.4	3.8	185	185	11.4
044	WS	F	75	6.0	175	120	17.9	6.6	170	105	23.6
045	BL	M	69	11.0	170	135	12.5	12.3	140	110	19.3
046	HL	M	85	13.0	170	110	11.1	13.0	155	100	12.2
047	RP	F	91	8.2	145	130	8.9	7.4	145	111	10.7
048	BC	M	75	16.0	200	140	16.5	16.5	165	130	28.6
049	DE	M	82	9.3	190	145	15.7	9.0	170	120	17.9
050	AS	F	98	5.2	220	170	8.2	5.7	200	155	7.7
051	MM	M	74	5.0	175	85	5.4	4.0	140	90	8.0
052	FB	M	100	4.4	150	170	11.8	4.4	132	149	13.7
053	RL	M	71	8.5	160	95	8.6	8.0	140	85	12.7
054	BS	M	94	12.5	180	130	10.9	12.5	150	115	15.2
055	LS	F	79	7.2	205	145	9.8	7.4	150	125	10.7
056	JC	F	82	8.0	195	145	11.1	9.4	140	115	10.7
057	CD	M	69	14.0	175	135	11.1	14.0	145	115	12.9
058	LD	F	62	10.5	200	175	10.9	13.5	190	160	12.5
059	NS	F	82	6.3	175	200	6.8	7.0	165	180	9.1
060	GB	M	90	9.9	170	120	10.7	10.2	135	100	14.8
061	AM	F	69	9.0	170	110	10.0	9.0	160	110	8.9
062	GL	M	79	14.5	200	150	11.4	14.0	180	90	10.0
063	AM	M	92	8.8	220	180	11.1	9.2	200	180	11.1
064	AH	M	87	3.4	200	150	7.5	2.6	190	130	7.9
065	BW	M	69	14.0	175	115	20.7	14.0	165	125	29.3
066	MM	M	61	19.5	160	90	10.4	19.0	155	80	12.9
067	SF	F	23	22.0	145	130	18.6	23.0	140	120	22.2
068	KR	F	31	13.0	140	130	16.4	13.8	120	130	25.4
069	NG	F	24	21.0	125	105	15.0	23.5	110	100	22.2
070	JG	F	30	21.8	150	140	12.2	21.8	130	120	17.5
071	AV	F	20	18.0	110	115	8.8	22.0	100	90	18.2
072	TC	F	29	18.0	170	110	14.7	20.0	165	105	14.7
073	ET	F	31	19.5	155	140	15.7	19.5	150	125	18.6
074	TB	M	27	21.0	155	115	15.7	21.5	130	115	20.7
075	PV	F	27	23.5	140	130	17.2	25.8	120	110	28.6
076	SM	M	23	22.0	115	105	19.3	22.0	110	90	33.6
077	JB	M	25	22.5	150	125	18.2	23.5	150	85	26.5
078	KM	F	29	13.3	180	120	10.7	13.5	170	110	11.1
079	TB	M	26	24.5	145	95	11.4	22.0	150	90	14.7
080	JM	M	27	11.8	155	115	10.7	10.0	144	102	19.5
081	MC	M	23	16.5	135	95	17.5	17.0	105	90	35.0
082	BL	F	30	16.8	165	110	10.2	17.0	145	100	12.0
083	JJ	M	30	19.0	165	95	7.9	19.5	160	75	10.7
084	SN	F	26	21.0	130	125	9.5	21.3	130	115	10.4
085	JS	M	31	28.0	145	125	16.1	28.0	110	105	29.3
086	CD	M	28	18.0	140	120	16.4	16.5	140	110	21.5

Table A3 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	RESTING M-wave (Mv)	RESTING CT (ms)	RESTING 1/2RT (ms)	RESTING P_t (N.m)	POTENTIATED M-wave (Mv)	POTENTIATED CT (ms)	POTENTIATED 1/2RT (ms)	POTENTIATED P_t (N.m)
087	MH	M	27	24.0	140	110	18.2	26.3	140	90	22.2
088	PC	M	28	0.0	0	0	0.0	0.0	0	0	0.0
089	KB	F	22	0.0	0	0	0.0	0.0	0	0	0.0
090	NK	F	29	0.0	0	0	0.0	0.0	0	0	0.0
091	JB	M	32	0.0	0	0	0.0	0.0	0	0	0.0
092	JK	M	29	0.0	0	0	0.0	0.0	0	0	0.0
093	TV	M	28	20.0	135	95	18.6	20.8	110	80	25.1
094	DB	M	45	22.0	200	155	17.9	22.5	170	140	21.1
095	RM	M	45	18.5	175	120	17.5	21.5	140	110	39.3
096	PY	F	41	9.8	170	130	15.0	10.8	155	115	18.6
097	BV	M	40	12.0	170	135	17.2	12.0	170	130	28.5
098	CC	M	44	18.8	180	125	20.9	17.5	150	115	32.8
099	BC	F	40	15.5	190	170	10.9	16.5	165	150	14.7
100	JD	M	45	15.0	165	115	12.8	13.5	165	115	18.5
101	MM	M	40	21.0	155	115	17.9	21.5	130	115	29.7
102	EG	F	49	10.0	190	130	10.4	9.0	195	118	12.5
103	AP	F	43	15.5	170	140	14.3	15.5	150	130	17.9
104	EK	M	44	19.5	140	105	20.0	19.0	150	95	22.9
105	DP	M	43	14.0	175	120	9.7	14.0	160	90	11.4
106	HL	F	42	21.5	190	130	13.6	22.0	185	115	13.6
107	SK	F	47	20.0	170	140	18.6	21.0	165	130	23.6
108	JB	F	41	12.0	175	150	19.0	12.0	180	125	22.2
109	GH	M	42	23.5	155	110	12.5	22.0	130	100	23.6
110	AM	M	49	21.5	170	120	16.5	22.0	130	110	27.2
111	MM	F	44	14.5	180	140	14.1	15.0	165	115	17.2
112	LC	F	41	9.2	175	120	17.5	7.0	125	110	21.5
113	DN	F	52	21.5	180	135	11.6	21.5	185	130	12.9
114	MM	F	100	6.1	230	170	2.9	6.1	196	149	2.9
115	HN	M	98	7.4	220	160	13.6	7.8	200	125	13.9
116	MH	F	87	6.0	205	190	8.2	6.0	190	170	13.9

Table A4. Individual Data for Maximal Voluntary Contractile Strength (MVC) of the Dorsiflexor (DF) and Plantarflexor (PF) Muscles

Subject (#)	(Init)	Sex	Age (Yr)	DF MVC (N.m)	PF MVC (N.m)
001	AM	F	70	24.0	70.1
002	CM	M	80	30.0	164.5
003	BM	M	78	32.9	135.9
004	HM	M	73	37.2	139.4
005	MM	F	66	25.5	146.6
006	HG	M	82	25.2	93.7
007	RP	M	80	27.5	70.1
008	SW	M	75	32.9	139.4
009	MD	F	78	16.4	44.3
010	AP	M	82	29.2	107.3
011	DL	F	82	18.3	93.0
012	EC	F	71	15.4	114.4
013	DM	F	67	23.5	65.8
014	RL	M	70	24.3	85.8
015	HF	M	82	21.7	96.5
016	DK	F	69	24.0	93.0
017	AP	M	73	20.0	78.7
018	VW	F	66	20.6	114.4
019	JG	M	68	32.9	128.7
020	JW	M	73	26.3	128.7
021	ME	F	72	23.5	100.1
022	CE	M	73	29.2	121.6
023	JR	M	75	54.3	146.6
024	MM	M	60	31.5	143.0
025	KD	M	73	37.2	164.5
026	JO	M	71	38.6	146.6
027	SP	M	67	44.3	132.3
028	JH	M	61	51.5	168.0
029	BW	M	77	28.6	89.4
030	MC	F	62	22.9	89.4
031	JC	M	68	39.3	128.7
032	MW	F	62	28.0	125.1
033	DM	M	62	31.5	168.0
034	MR	F	76	24.6	114.4
035	MH	F	77	18.9	84.0
036	RE	M	61	35.0	107.3
037	LS	M	65	27.2	153.7
038	AS	F	63	18.3	80.1
039	TL	F	70	21.2	125.1
040	RC	M	69	25.2	96.5
041	MV	F	63	28.0	89.4
042	BM	M	74	32.0	85.8
043	NN	F	87	17.2	54.3

Table A4 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	DF MVC (N.m)	PF MVC (N.m)
044	WS	F	75	22.6	114.4
045	BL	M	69	37.2	135.9
046	HL	M	85	31.5	77.2
047	RP	F	91	20.0	62.9
048	BC	M	75	38.6	177.0
049	DE	M	82	35.8	139.4
050	AS	F	98	13.7	33.8
051	MM	M	74	26.9	100.1
052	FB	M	100	14.9	82.2
053	RL	M	71	28.6	103.7
054	BS	M	94	17.2	85.8
055	LS	F	79	27.2	75.8
056	JC	F	82	21.2	65.8
057	CD	M	69	42.9	105.5
058	LD	F	62	21.7	78.7
059	NS	F	82	18.3	52.9
060	GB	M	90	20.6	85.8
061	AM	F	69	25.2	77.2
062	GL	M	79	18.3	94.7
063	AM	M	92	18.9	77.2
064	AH	M	87	12.9	44.3
065	BW	M	69	42.9	173.4
066	MM	M	61	29.7	128.7
067	SF	F	23	23.5	128.7
068	KR	F	31	19.2	157.3
069	NG	F	24	30.0	107.3
070	JG	F	30	28.0	141.2
071	AV	F	20	28.6	103.7
072	TC	F	29	32.0	75.1
073	ET	F	31	28.6	128.7
074	TB	M	27	54.3	153.7
075	PV	F	27	29.7	168.0
076	SM	M	23	40.0	193.1
077	JB	M	25	38.6	194.8
078	KM	F	29	27.5	60.8
079	TB	M	26	37.2	100.1
080	JM	M	27	50.8	153.7
081	MC	M	23	48.6	203.8
082	BL	F	30	27.5	78.7
083	JJ	M	30	37.2	143.0
084	SN	F	26	18.0	96.5
085	JS	M	31	44.3	178.8
086	CD	M	28	50.1	164.5
087	MH	M	27	41.5	221.7
088	PC	M	28	0.0	0.0
089	KB	F	22	0.0	0.0
090	NK	F	29	0.0	0.0

Table A4 Cont'd

Subject (#)	(Init)	Sex	Age (Yr)	DF MVC (N.m)	PF MVC (N.m)
091	JB	M	32	0.0	0.0
092	JK	M	29	0.0	0.0
093	TV	M	28	35.8	175.2
094	DB	M	45	28.0	144.8
095	RM	M	45	41.5	207.4
096	PY	F	41	22.9	143.0
097	BV	M	40	36.2	171.2
098	CC	M	44	38.0	218.7
099	BC	F	40	15.2	91.3
100	JD	M	45	35.8	137.9
101	MM	M	40	38.6	202.0
102	EG	F	49	28.6	103.7
103	AP	F	43	22.6	100.1
104	EK	M	44	42.2	160.9
105	DP	M	43	35.8	128.7
106	HL	F	42	31.5	150.2
107	SK	F	47	30.9	143.0
108	JB	F	41	22.3	157.3
109	GH	M	42	34.3	137.6
110	AM	M	49	41.5	203.8
111	MM	F	44	22.9	110.8
112	LC	F	41	37.2	168.0
113	DN	F	52	24.0	100.1
114	MM	F	100	5.9	16.1
115	HN	M	98	28.6	93.0
116	MH	F	87	18.6	50.1

Table A5. Individual Data for Resting Isometric Twitch Characteristics of the Lateral Gastrocnemius (LG), Medial Gastrocnemius (MG), Soleus (SOL) and Entire Plantarflexor (PF) Muscles. Variables are Contraction Time and One-half Relaxation Time

Subject (#)	(Init)	Sex	Age (Yr)	CONTRACTION TIME (ms) LG	MG	SOL	PF	1/2 RELAXATION TIME (ms) LG	MG	SOL	PF
007	RP	M	80	120	150	160	205	130	170	170	125
011	DL	F	82	110	160	160	185	170	140	230	140
012	EC	F	71	120	130	180	175	120	125	220	175
015	HF	M	82	125	110	165	165	130	100	190	150
025	KD	M	73	140	135	175	155	90	120	155	100
032	MW	F	62	140	130	170	200	190	150	215	135
034	MR	F	76	90	135	140	195	140	125	195	140
043	NN	F	87	135	125	145	165	200	140	260	180
044	WS	F	75	110	120	160	145	100	90	195	115
045	BL	M	69	110	130	160	160	120	130	190	120
046	HL	M	85	110	120	130	160	100	95	145	100
047	RP	F	91	110	145	205	145	95	110	240	130
048	BC	M	75	145	140	190	200	150	125	170	140
051	FB	M	100	90	110	140	145	100	195	170	185
061	AM	F	69	140	150	200	200	120	105	215	150
067	SF	F	23	120	115	170	150	130	110	210	130
068	KR	F	31	100	110	160	145	105	105	145	110
069	NG	F	24	100	120	125	125	90	75	175	105
074	TB	M	27	100	130	185	155	90	110	200	115
075	PV	F	27	100	140	170	135	110	145	160	145
085	MO	M	23	95	115	130	130	95	125	125	120
088	PC	M	28	95	105	150	130	60	90	130	110
089	KB	F	22	105	145	160	135	130	140	145	145
090	NK	F	29	115	125	175	150	115	120	160	115
091	JB	M	32	90	80	165	140	100	105	205	145
092	JK	M	29	85	90	145	140	55	85	115	100
093	TV	M	28	95	110	140	140	105	85	120	105

Table A6. Individual Data for Cross-sectional Area of the Gastrocnemius and Soleus Muscles

Subject (#)	(Init)	Sex	Age (Yr)	Cross-sectional Area (cm^2) Gastrocnemius	Soleus
011	DL	F	82	11.28	12.02
043	NN	F	87	10.10	11.26
046	HL	M	85	17.13	18.61
047	RP	F	91	9.99	9.90
050	AS	F	98	5.63	9.35
052	FB	M	100	10.96	15.17
056	JC	F	82	11.66	13.18
060	GB	M	90	14.10	16.23
063	AM	M	92	11.25	11.54
064	AH	M	87	12.47	12.67
067	SF	F	23	17.85	13.64
068	KR	F	31	13.63	14.37
075	PV	F	27	16.38	15.26
076	SM	M	23	18.67	23.50
078	KM	F	29	14.53	18.82
080	JM	M	27	15.57	16.58
082	BL	F	30	15.44	16.34
083	JJ	M	30	21.86	20.11
085	JS	M	31	17.39	17.65
093	TV	M	28	14.92	16.28

APPENDIX C

Reliability of Measurements Made on Two Separate Days

Measure	Mean 1	Mean 2	ME(V) %	Pairs of Observations
Passive Tension				
At 10°D (N.m)	2.8	2.5	10.0	7
At 30°P (N.m)	1.7	2.0	17.9	7
Range of motion (° DF)	31.3	33.0	9.0	7
PF Resting Twitch				
M-Wave (Mv)	12.0	11.9	11.0	7
CT (ms)	187.1	180.0	5.4	7
1/2 RT (ms)	133.6	131.4	7.2	7
P_t (N.m)	13.4	12.2	10.8	7
PF Potentiated Twitch				
M-Wave (Mv)	12.6	12.5	8.8	6
CT (ms)	155.8	147.5	5.8	6
1/2 RT (ms)	107.5	117.5	13.0	6
P_t (N.m)	16.8	18.5	12.9	6
DF MVC	25.9	26.5	3.2	9
PF MVC	98.6	100.7	11.1	9
Gastrocnemius and Soleus CSAs (cm^2)	16.93	17.84	5.8	10

For reliability assessments, all subjects were over 60 yr of age, except in the case of ultrasound measurements, for which young adults were used. There was at least a week between tests. None of the means were significantly different.

The method error statistic for measurements made twice on a group of subjects is calculated using the formula:

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

in which d = difference between the 2 measurements made on each subject, $\bar{d}$ = the mean difference and n = number of subjects.

ME was expressed as a coefficient of variation via the formula

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