Contractile changes in opposing muscles of the human ankle joint with aging

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VANDERVOORT, ANTHONY A., AND ALAN J. McCOMAS. *Contractile changes in opposing muscles of the human ankle joint with aging.* J. Appl. Physiol. 61(1): 361–367, 1986.—The effects of aging on maximal voluntary strength and on the isometric twitch were determined in the ankle dorsiflexor and plantarflexor muscles of 111 healthy men and women aged 20–100 yr. Men were found to be stronger than women at all ages. In both sexes, the average values for maximum voluntary strength of the dorsiflexors and plantarflexors began to decline in the 6th decade. Although the absolute loss of strength was greater for the plantarflexor muscles, the relative losses were similar in the two muscle groups. During maximum voluntary effort, stimulation of motor nerves produced no additional torque in the majority of elderly men and women, indicating that these subjects remained able to utilize their descending motor pathways for optimal muscle activation. Comparisons of muscle compound action potentials, twitch torques, and muscle cross-sectional areas suggested that a decrease in excitable muscle mass was entirely responsible for the lower strength of the elderly. An additional effect of aging was the gradual prolongation of twitch contraction and half-relaxation times throughout the adult life-span.

muscle strength; isometric contraction; twitch; leg; cross-sectional area; age

LOSS OF VOLUNTARY STRENGTH is a well-known feature of aging (6, 10, 16), yet it is not clear at which age this impairment begins (22). Nor is it established whether this decrease is entirely due to a loss of excitable muscle mass (7, 8) or whether impairment of descending motor pathways constitutes an additional factor. In the present study, this last question has been addressed by interpolating motor nerve stimuli during maximal voluntary contractions. If such stimuli evoked additional torque, it followed that some motor units had not been recruited during the voluntary contraction or else were firing at suboptimal frequencies for torque development (1, 21).

In seeking to resolve these issues we have chosen to study the dorsiflexor and plantarflexor muscles of the ankle for two reasons. First, since all the subjects were walking, these muscles would be expected to show less evidence of disuse than, for example, muscles employed in heavy manual work. Secondly, in young adults the dorsiflexor and plantarflexor muscles have quite striking physiological differences (2); it was therefore of interest to enquire whether aging affected the two muscle groups to similar extents as, for example, in prolongation of the twitch (10). A preliminary report of this research has been made elsewhere (26).

METHODS

Subjects. Subjects were healthy volunteers from the community between the ages of 20 and 100 yr; the majority were over the age of 60. Depending on their ages and sex, the subjects were divided into five groups; the number of subjects, mean height, and mean weight of each male and female group are shown in Table 1. Subjects recruited for the "young" (20–32 yr) and "middle-aged" (40–52 yr) groups were no more than moderately active; all of the old people walked daily without aid and were living at home. The study carried the approval of the Ethics Committee at McMaster University.

Measurement of muscle contractile properties. Isometric torques generated about the ankle joint by the dorsiflexor or plantarflexor muscles were recorded using the leg holder described by Marsh et al. (18). The subject's dominant foot (usually the right) was strapped to the footplate; the inclination of the foot could be altered by rotating the footplate about an axis that corresponded to that of the ankle joint. Torques acting on the footplate were sensed by strain gauges mounted on a rigid bar underneath the plate. The electrical signals from these gauges were amplified and displayed on a storage oscilloscope (Hewlett-Packard type 141B) from which measurements were made. The system was linear for torques up to 250 N·m, and the resonant frequency of the footplate was 85 Hz.

The footplate was adjusted to place the muscle group under study at its optimal length for tension development, according to the earlier investigations of Marsh et al. (18) and Sale et al. (23). For measurements on the dorsiflexor muscle group, the ankle was placed in 30° of plantarflexion (30° of downward rotation from the neutral position, defined as perpendicularity of the sole of the foot to the long axis of the tibia). The test position for the plantarflexor group was 10° of dorsiflexion. Tests of muscle contraction were conducted in the order of their presentation in METHODS.

Isometric twitch properties. The skin was prepared for electrode attachment by rubbing it vigorously with alcohol and then with conducting cream. Stimulating electrodes for evoking maximal twitches were two strips of

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TABLE 1. *Number and physical attributes of male and female subjects in different age groups*

		Age group, yr				
		20–32	40–52	60–69	70–79	80–100
No. of subj	M	11	10	13	16	13
	F	11	10	10	9	8
Age, yr	M	26.8±2.5	43.7±2.7	65.3±3.7	74.0±2.5	87.2±6.9
	F	27.3±3.6	44.0±4.0	64.9±2.9	74.2±3.5	88.6±7.2
Ht, cm	M	176.2±7.5	176.8±5.9	172.4±5.6	174.7±9.4	167.4±3.7
	F	160.1±6.0	162.9±6.5	159.7±7.6	162.4±5.5	155.4±6.1
Wt, kg	M	72.8±8.8	77.5±12.4	73.8±12.0	71.5±9.3	66.8±5.9
	F	54.5±6.5	66.0±10.3	60.5±7.8	58.8±9.9	53.5±8.2

Values are means ± SD.

aluminum foil, ~3×5 cm, connected to a constant voltage stimulator (Devices type 3072). For the dorsiflexor groups, the stimulating cathode was attached to the skin overlying the common peroneal nerve at the neck of the fibula and the anode was placed 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 supramaximal stimulating pulses were too brief (50–100 μs) for anodal block to interfere with impulse propagation from the cathode to tibialis anterior. For the plantarflexor muscle group, a pair of stimulating electrodes was placed snugly against the skin in the popliteal fossa to lay over the tibial nerve.

M waves (muscle compound action potentials) were led off the dorsiflexor group by a stigmatic-recording electrode on the skin over the belly of tibialis anterior; a reference electrode was placed over the tendon of the same muscle at the level of the ankle. For recording plantarflexor M waves, the respective positions of stigmatic and reference electrodes were over the soleus, just below the separation of the gastrocnemius muscle bellies, and over the Achilles tendon. Recording electrodes were Beckman silver cups, 7 mm in diam. The ground electrode was a strip of silver foil placed between the stimulating anode and the stigmatic recording electrode. Electromyographic (EMG) signals were fed through a preamplifier with a pass band of 10 Hz to 1 kHz before being displayed on the storage oscilloscope.

Twitch times were measured on a digital analyzer (Hewlett-Packard type 5408B), using a differentiating circuit to identify the onset of the twitch and the moment when it reached its maximum torque. Subjects were taught to relax their muscles by listening to the 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 potentiate the twitch (27). Postactivation potentiation was examined by eliciting a twitch after a 5-s bout of maximal voluntary muscle activity (timed by a light).

In some subjects, comparisons were made of the twitch properties of different parts of the triceps surae (soleus, medial and lateral gastrocnemius muscles). In these experiments submaximal stimuli were applied through surface electrodes placed over the respective muscle bellies in positions where thresholds were lowest. Other muscles were monitored by visual inspection and EMG recordings to ensure that stimulation was restricted to the muscle under study. Representative twitches were thus obtained with clearly defined differences between each muscle (25).

Maximum voluntary strength. Subjects were given several attempts to achieve as large a torque as possible during voluntary muscle contraction (MVC). During the MVC, a supramaximal stimulus was applied to the motor nerve to assess whether the subject was activating his or her muscles optimally (1, 21). This technique also proved useful as a means for motivating subjects if incomplete muscle activation was present. Additional forms of encouragement were EMG biofeedback from the loudspeaker, the oscilloscope record of the torque output, and verbal encouragement. 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 over several trials.

Motor unit estimates. Numbers of functioning motor units were estimated in both soleus muscles of five of the oldest subjects (80–100 yr).

The stigmatic recording electrode consisted of a strip of silver foil, 4×6 cm, attached to the skin in the posterior midline of the leg, 3 cm below the gastrocnemii. The reference electrode was another piece of foil placed over the Achilles tendon; the stimulating electrodes were silver discs applied over the tibial nerve in the popliteal fossa. As the stimulus intensity was gradually increased from a subthreshold value, the responses on the oscilloscope storage screen were seen to become larger in an incremental manner; each increment was attributed to the excitation of an additional motor unit. The average peak-to-peak amplitude of the increments was then compared with the maximal M wave to yield an estimate of the number of functioning motor units. The assumptions inherent in the method have been discussed in detail elsewhere (19, 20); in particular, it is recognized that muscles close to soleus and supplied by the tibial nerve, may have contributed to the estimates.

Muscle cross-sectional areas. Subgroups of young and very old adults, with comparable body sizes, were selected for this part of the investigation. Cross-sectional areas of the leg, at the level of maximum calf girth, were made with a B-scanner ultrasound imaging system (Picker). The outlines of the gastrocnemius and soleus muscles were identified on the photograph through the identification of borderlines created at muscle-connective tissue interfaces. Delineated muscle areas were then measured on a computerized digitizing board (Numonics).

Data analysis. An analysis of variance was used to assess the influence of the two grouping factors, age and sex, on the measures of neuromuscular function. Group means and SD were calculated to allow for assessment of within-group variance and for the analysis of trends in the data. For some of the variables, data were normalized with respect to those of young adults in order to clarify changes with age. Significant interactions between the effects of age and sex were investigated further with Newman-Keul's multiple-range test of significance for differences between several means. An X^2 test was used to test the significance of differences in motor unit activation. The reliability of each measurement technique was assessed by comparing values determined for 6–10 subjects on two different days. The mean differences between the paired results were 5% or less, with the exception of twitch torque and potentiation (9 and 10%, respectively).

RESULTS

Age and voluntary strength. The torques developed during maximum voluntary dorsiflexion and plantarflexion of the ankle are shown in Tables 2 and 3, respectively; separate means have been given for male and female subjects in each age group. It was found that males were significantly stronger than females for both types of contraction at all ages studied ($P < 0.001$).

The effect of age was to cause a reduction in voluntary torque in both sexes. In the oldest group of men (80–100 yr) the mean dorsiflexor and plantarflexor torques were 56 and 55%, respectively, of those in the youngest group (20–32 yr), whereas the corresponding values for women were 63 and 48%. However, when the values for subjects in the youngest and middle-aged (40–52 yr) groups were compared the voluntary torques were very similar, with only dorsiflexion in men showing a significant decrease ($P < 0.05$). These last findings indicated that aging was not associated with progressive weakness beyond young adulthood, but rather that there was a critical later age at which strength began to decline. This interpretation was supported by another type of analysis in which the maximum dorsiflexor and plantarflexor torques of individuals were expressed as percentages of the mean values for the youngest group of subjects of the same sex; these results are shown in Fig. 1. Correlation analysis showed no significant relationship between normalized strength and age for subjects aged 20–52 yr ($r = 0.043$), whereas a significant negative linear relationship could be demonstrated for subjects aged 60–100 yr ($r = -0.604$; $P < 0.001$). The intersection between the lines drawn for the results in the two groups of subjects (aged 20–52 and 60–100 yr, respectively) corresponded to an age of 53 yr.

Twitch interpolation during MVC. In assessment of the results for maximum voluntary strength it was important to establish whether or not the subjects had been able to activate their motor units fully; i.e., by causing all motoneurones to discharge at optimal frequencies for tension development. The degree of motor unit activation was tested by applying a maximal stimulus to the peroneal nerve during voluntary dorsiflexion of the ankle or to the tibial nerve during plantarflexion. In the case of the dorsiflexor muscles, there was no evidence of twitch responses superimposed on the voluntary force recordings in any of the subjects, irrespective of age. These results indicated that motor unit activation had been complete and that the measurements of voluntary strength reflected the excitable mass of the dorsiflexor muscles accurately. Similar results were obtained for the plantarflexor muscles in 55 of the 69 subjects aged 60 or more yr and in 39 of the 42 younger subjects; the difference between the two groups in the incidence of complete activation was not significant. In addition, it was unlikely that the "true" capacity for plantarflexion differed much from the observed values in the 17 subjects with interpolated twitch responses, since the latter were all small in relation to the control twitches recorded at rest (cf Belanger and McComas, Ref. 1).

Age and twitch response. The maximal isometric twitch torques are shown in Tables 2 and 3 for the dorsiflexor and plantarflexor muscles, respectively. These results

TABLE 2. *Effects of age on contractile properties of ankle dorsiflexor muscles in male and female subjects*

		Age group, yr				
		20–32	40–52	60–69	70–79	80–100
MVC, N·m	M	43.5±6.5	37.2±4.3	36.2±7.6	31.6±8.6	24.2±7.0
	F	26.6±4.5	25.8±6.3	23.8±3.1	21.5±3.9	16.7±4.9
P_t, N·m	M	4.2±1.5	4.5±1.2	3.3±1.4	3.3±1.3	2.6±0.8
	F	2.7±1.3	3.7±0.9	2.8±1.0	1.8±0.9	1.7±0.8
CT, ms	M	101±7	111±13	104±11	115±15.1	125±21.8
	F	96±8	113±10	115±9	110±12.5	128±10
½RT, ms	M	84±11	100±15	102±19	122±23	125±32
	F	84±13	110±19	120±16	119±28	131±29
M wave, mV	M	9.4±2.6	9.7±1.5	7.0±1.9	7.8±3.1	5.4±1.6
	F	9.1±2.6	10.5±2.3	7.9±4.0	6.3±2.8	5.2±2.0
PAP, control	M	1.71±0.21	1.45±0.15	1.42±0.31	1.31±0.23	1.31±0.21
	F	1.75±0.45	1.46±0.30	1.35±0.20	1.35±0.32	1.28±0.31

Values are means ± SD. MVC, maximum voluntary contractions; P_t, maximum twitch torque; CT, contraction time; ½RT, half-relaxation time; PAP, postactivation potentiation. See text for significance of differences between means.

TABLE 3. *Effects of age on contractile properties of ankle plantarflexor muscles in male and female subjects*

		Age group, yr				
		20–32	40–52	60–69	70–79	80–100
MVC, N·m	M	171±34	171±34	136±25	121±31	94±30
	F	113±35	127±28	96±25	94±27	54±23
P_t, N·m	M	15.5±3.8	16.3±3.5	13.4±4.2	13.4±4.1	11.9±2.3
	F	13.6±3.4	14.5±3.1	11.9±3.2	13.0±3.5	8.6±3.0
CT, ms	M	144±13	169±16	170±13	178±19	186±22
	F	146±21	179±8.4	182±11	183±23	195±27
½RT, ms	M	109±12	122±14	117±17	133±33	144±21
	F	123±12	139±14	133±21	143±27	169±30
M wave, mV	M	20.7±4.4	18.6±3.8	13.3±4.1	12.2±4.2	9.5±3.7
	F	18.9±3.5	15.0±4.8	10.5±4.6	8.8±2.6	6.4±1.7
PAP, /control	M	1.52±0.27	1.56±0.35	1.29±0.19	1.22±0.24	1.15±0.17
	F	1.35±0.32	1.20±0.10	1.12±0.16	1.12±0.21	1.17±0.25

Values are means ± SD. MVC, maximum voluntary contraction; P_t, maximum twitch torque; CT, contraction time; ½RT, half-relaxation time; PAP, postactivation potentiation. See text for significance of differences between means.

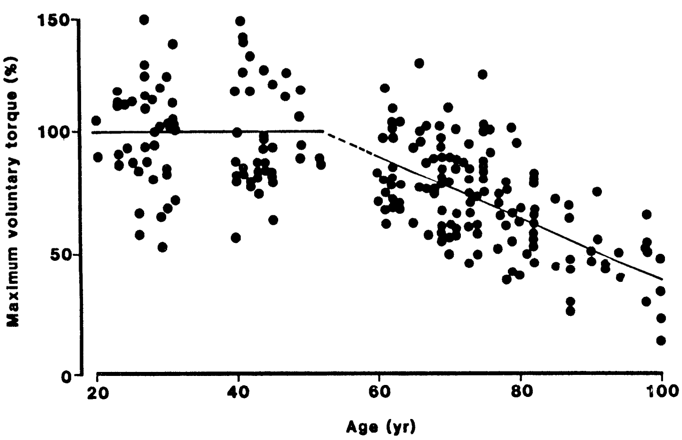

FIG. 1. Maximum voluntary dorsiflexor and plantarflexor torques in 111 subjects, expressed as percentages of mean values for youngest groups (20–30 yr) of men and women, respectively. Regression line for subjects ages 60 yr and over was $y = -1.29x + 169.2$ ($r = -0.604$, $P < 0.001$). *Horizontal line* for subjects aged 52 yr or less reflects lack of significant influence of age ($r = -0.043$).

were similar to the voluntary strength measurements in that they showed higher values for men than women at all ages and, in both sexes, a decline beyond middle age ($P < 0.001$). When the oldest group of men and women (80–100 yr) was compared with the youngest (20–32 yr), the mean losses in dorsiflexor and plantarflexor twitch torques amounted to 38 and 23%, respectively for males and to 37% in both instances for females. Since twitch torque was affected by age to a lesser extent than maximum voluntary torque, the ratio of the latter to the former became smaller in older subjects, particularly in the plantarflexor muscles (from 11.5 ± 2.7 to 7.7 ± 1.3 in men and from 8.5 ± 2.2 to 6.2 ± 1.2 in women; $P < 0.001$ for effects of age and sex).

Twitch durations were also affected by age and sex. In the plantarflexor muscles, though not in the dorsiflexors, both the contraction and half-relaxation times were significantly longer in women than men ($P < 0.05$ and $P < 0.001$, respectively) (Table 3). With increasing age, the contraction and half-relaxation times became prolonged in both muscle groups and in both sexes ($P < 0.001$) (Fig. 2).

A further analysis was made of the effects of age on twitch duration in the plantarflexor muscles; the technique involved stimulating the soleus and the two gastrocnemius muscle bellies separately (see METHODS). As noted in a previous study (25) the contraction and half-relaxation times were shortest in the lateral gastrocnemius and longest in the soleus. When the results for the oldest and youngest subjects were compared, it was found that aging prolonged the contraction times of both gastrocnemii significantly in men and women but was without an effect on the soleus (Table 4). The mean half-relaxation times of all three muscles were significantly longer in the older subjects ($P < 0.001$) and in women ($P < 0.02$). Twitch potentiation was also susceptible to aging, being significantly smaller in the dorsiflexor and plantarflexor muscles of the older subjects ($P < 0.001$) (Tables 2 and 3).

The final part of the twitch analysis was concerned with the maximal amplitude of the associated M wave. As with the observations on voluntary and twitch torques, significant decreases were found in subjects beyond middle age (Tables 2 and 3). In extreme old age (80–100 yr) the largest reductions in M-wave response took place in the plantarflexor muscles, the mean values for men and women being 46 and 34% of those in young adults; for dorsiflexor muscles the corresponding values were 57% in both sexes.

Muscle cross-sectional areas. Cross-sectional areas of the calf muscles were compared between young and very old adults based on ultrasound images of the lower leg. Males differed from females in having significantly greater ($P < 0.01$) values for the triceps surae complex (gastrocnemii and soleus), whereas elderly men and women (aged 82–100 yr) had significantly smaller areas than young adults ($P < 0.001$). The mean values were 36.5 ± 5.3, 31.1 ± 2.0, 28.0 ± 5.1, and 20.9 ± 3.8 cm^2 for young men, young women, old men, and old women, respectively. These reductions in cross-sectional area were less than the decreases in strength of voluntary plantarflexion of the elderly; therefore, calculated ratios of torque per unit area (Fig. 3) were significantly lower ($P < 0.01$). These ratios did not show a sex difference (Fig. 3).

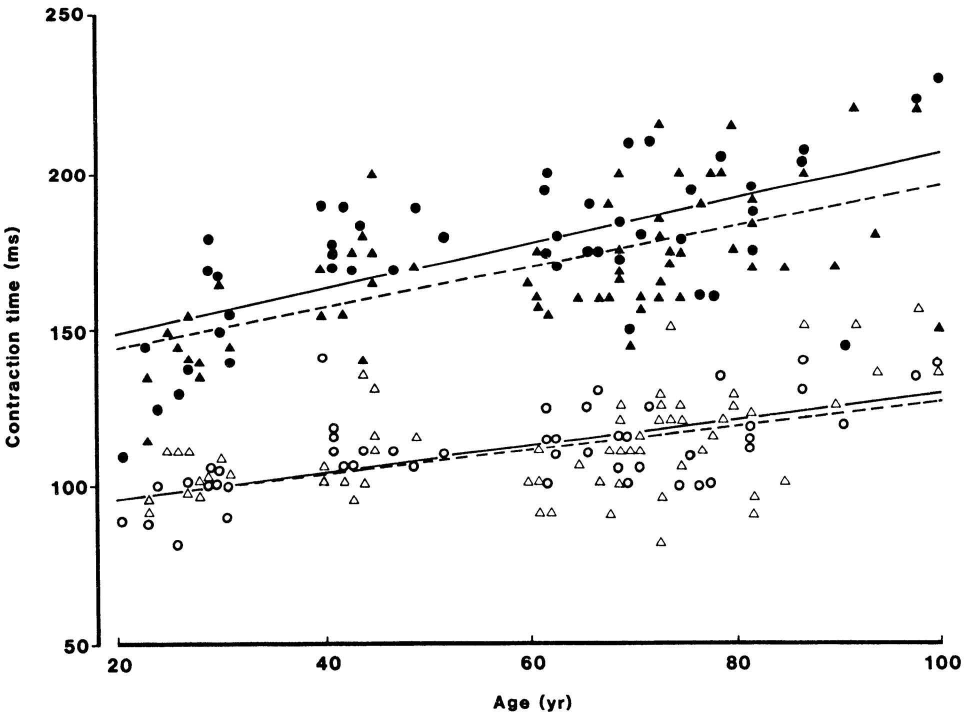

FIG. 2. Twitch contraction times as functions of age in dorsiflexor and plantarflexor muscles. In both sexes the 2 muscle groups showed significant correlations with age ($P < 0.001$). Symbols: *closed triangles*, male plantarflexor; *open triangles*, male dorsiflexor; *closed circles*, female plantarflexor; *open circles*, female dorsiflexor. Regression lines plotted for each muscle group using continuous lines for women and interrupted lines for men, using following formula: $y = 0.711x + 134.5$ (female plantarflexors, $r = 0.644$); $y = 0.637x + 130.9$ (male plantarflexors, $r = 0.637$); $y = 0.30x + 88.7$ (male dorsiflexors, $r = 0.487$).

TABLE 4. *Contraction and half-relaxation times of muscle bellies comprising triceps surae in young and old subjects*

Parameter	Muscle	Men		Women	
		Young	Old	Young	Old
Contraction time, ms	LG	93±5	123±19	107±9	116±17
	MG	105±18	131±16	126±14	135±14
	SOL	153±20	165±24	160±18	166±22
	PF	139±9	174±24	140±10	173±22
Half-relaxation time, ms	LG	84±21	118±20	113±15	145±43
	MG	100±16	130±35	116±26	128±21
	SOL	149±42	176±22	166±24	222±24
	PF	116±16	134±29	125±18	145±24

Values are means ± SD. LG, lateral gastrocnemius; MG, medial gastrocnemius; SOL, soleus; PF, entire plantarflexor muscle group. See text for significance of differences between means.

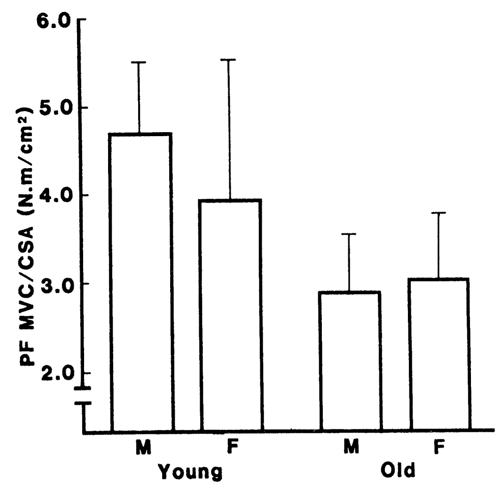

FIG. 3. PF strength relative to muscle CSA in young and old men and women. Cross-sectional areas (CSAs) of soleus and gastrocnemius muscles were measured using ultrasound imaging. Young adults, aged 23–31 yr, had significantly higher ratios than old adults, aged 82–100 yr ($P < 0.01$). Sex was not a significant factor. Mean and SD are shown; $n = 5$/group.

Motor unit estimates. In five of the oldest subjects (aged 80–100 yr) the number of functioning motor units was estimated in both soleus muscles using graded stimulation to evoke presumptive motor unit responses (19, 20). The mean value obtained, 283 ± 83 units, represented a 70% reduction from the value for young and middle-aged adults (19).

DISCUSSION

There have been many previous investigations of human voluntary strength as a function of age (for review see Grimby and Saltin, Ref. 12), but special techniques are needed to establish whether the observed results represent the true force-generating capacities of the muscles under study. In the present study, we have tested the functional integrity of the descending motor pathways in the central nervous system by interpolating maximal indirect stimuli during the voluntary contractions and searching for increments in torque (cf. Belanger and McComas, Ref. 1). The results have shown that, perhaps contrary to expectation, most elderly subjects can fully recruit their motor unit populations and excite motoneurones at optimal frequencies for tension development. The voluntary torque values obtained in the elderly subjects may therefore be regarded as accurate reflections of excitable muscle mass. The lower strength values observed in females relative to males were attributable to smaller muscle size; strength per cross-sectional area values were equivalent for the sexes.

In the study, significant reductions in voluntary strength were observed in the elderly and the relative declines were similar in the dorsiflexors and plantarflexors of the ankle and in both sexes. This decrease in average strength did not begin until the 6th decade, however, and preservation of plantarflexor muscle strength in middle age has also been found by Fugl-Meyer et al. (11) and by Belanger et al. (2); a similar finding has also been reported for handgrip strength (22). In interpreting the falling portion of the age-strength curve it must be recognized that, beyond the age of 70 yr, the population of subjects becomes increasingly biased toward those possessing physical attributes favoring longevity. Our data indicate that, by the time the normal life expectancy of ~75 yr has been reached, voluntary strength has been reduced to ~80% of that in younger adults. Such a modest decline in strength would not be expected to interfere with most activities and this was borne out by the lifestyles of the men and women in this study. By the age of 90 yr, however, muscle strength was reduced to about half; whereas adequate for the activities of daily living, the remaining strength level might well be a contributing factor toward the poor ability to cope with physical stresses associated with such events as infections, accidents, and surgery.

The cause of the reduction in strength observed in the present study was unlikely to have been disuse, since the elderly subjects were all used to walking without assistance. One factor was probably muscle denervation, since estimates of functioning soleus motor units in five of the oldest subjects were reduced by more than two-thirds. On the basis of other studies (8, 19, 20) motor unit loss would not be expected to occur before the age of 60 yr, at a time when average voluntary strength had already begun to fall. It would therefore appear that factors other than denervation of entire motor units were implicated in the present results. Of interest is the recent report that old rat soleus muscles appeared to respond favorably to chronic exercise by developing sprouts from motor nerve terminals, a process that probably serves to maintain the effectiveness of the neuromuscular junction (24).

The decline in the cross-sectional areas of the gastrocnemius and soleus muscles with age was found to be less than the reduction in voluntary plantarflexor strength. Similar results have been reported by Young et al. (29) for the quadriceps muscles of elderly men but not for the same muscles in elderly women (28). Like ourselves, these authors employed ultrasonic imaging to determine muscle cross-sectional areas. The discrepancy between the strength and area measurements in the ankle and quadriceps muscles was probably due, in part, to the presence of increased amounts of connective tissue in the muscles of the elderly subjects (14, 17). Lexell et al. (17) estimated that there was a 24% reduction in the mean number of vastus lateralis muscle fibers in men aged 70–73 yr, a figure that accords well with the loss of strength found for similarly aged subjects in the present study. These authors did not find a significant decrease in fiber size in their elderly subjects, but mild selective atrophy of type II muscle fibers has been noted in other investigations (for review see Ref. 12).

Studies of electrically evoked human muscle strength as a function of age have been rare. Botelho et al. (4) investigated the adductor pollicis, and Campbell et al. (8) examined another small distal muscle, the extensor digitorum brevis. The study of Davies and White (10) is especially relevant to the present one, being concerned with the plantarflexor muscle group. These investigators were able to employ tetanic stimulation by using large electrode pads, but the twitch responses may have been contaminated by H-reflexes (13), since no recordings of the M waves were undertaken. All three studies, however, agreed with the present one in demonstrating a prolongation of the muscle twitch with advancing age. We have shown that, of the muscles comprising the triceps surae, lengthening of the twitch was most conspicuous in the gastrocnemii and was associated with a reduction in twitch potentiation. These changes might have been due to an increase in the proportion of tension developed by the type I (slow-twitch) muscle fibers, stemming from loss or atrophy of type II (fast-twitch) fibers (7, 24). However, although there are no data on changes in composition of the ankle musculature with aging, in the human lateral vastus muscle only minor alterations in fiber-type proportions have been demonstrated (12). Further, if this explanation were correct, both voluntary and electrically evoked torques should have been reduced in middle-aged adults, in view of the smaller specific tensions of type I fibers (cf. cat triceps surae, see Ref. 5), but this was not observed. It is unlikely that hypothyroidism was the cause of increased twitch times (15), since this condition has been found to affect only 1–2% of elderly community dwellers (9) and none of the subjects in the present study were taking thyroid medication. If slowing of muscle contraction, from whatever cause, was responsible for the prolonged twitches in elderly subjects, then the rate of rise of tetanic tension should have decreased. Tetanic stimulation was not employed in our studies and there is no information on this point in the investigations by Davies and White (10). Alternatively, if the rate of rise of tetanic tension is eventually shown to be unaltered in aging, then the prolonged twitches must be due to increases in active state duration and the Ca^{2+} regulatory system would be implicated.

Irrespective of its mechanism, the prolongation of the twitch in the elderly confers greater efficiency, in that lower frequencies of nerve impulses are needed to produce given amounts of torque. It would be of interest to compare firing frequencies of young and old muscles during sustained voluntary contractions and to determine whether neuromuscular transmission is as well maintained in the elderly as in young adults (3).

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