Motor unit firing rates and contractile properties in tibialis anterior of young and old men

DENISE M. CONNELLY,1 CHARLES L. RICE,1,2 MARTIN R. ROOS,1 AND ANTHONY A. VANDERVOORT1,3

1Department of Anatomy and Cell Biology, Faculty of Medicine, and 3School of Physical Therapy, Faculty of Health Sciences, The University of Western Ontario, London, Ontario, Canada N6A 3K7

Connelly, Denise M., Charles L. Rice, Martin R. Roos, and Anthony A. Vandervoort. Motor unit firing rates and contractile properties in tibialis anterior of young and old men. J. Appl. Physiol. 87(2): 843–852, 1999.—The effects of aging on motoneuron firing rates and muscle contractile properties were studied in tibialis anterior muscle by comparing results from six young (20.8 ± 0.8 yr) and six old men (82.0 ± 1.7 yr). For each subject, data were collected from repeated tests over a 2-wk period. Contractile tests included maximal voluntary contraction (MVC) with twitch interpolation and stimulated twitch contractions. The old men had 26% lower MVC torque (P < 0.01) than did the young men, but percent activation was not different (99.1 and 99.3%, respectively). Twitch contraction durations were 23% longer (P < 0.01) in the old compared with the young men. During a series of repeated brief steady-state contractions at 10, 25, 50, 75, and 100% MVC, motor unit firing rates were recorded. Results from ~950 motor unit trains in each subject group indicated that at all relative torque levels mean firing rates were 30–35% lower (P < 0.01) in the old subjects. Comparisons between young and old subjects’ mean firing rates at each of 10%, 50%, and MVC torques and their corresponding mean twitch contraction duration yielded a range of moderate-to-high correlations (r = −0.67 to −0.84). That lower firing rates were matched to longer twitch contraction durations in the muscle of old men, and relatively higher firing rates were matched with shorter contraction times from the young men, indirectly supports the neuromuscular age-related remodeling principle.

Con naturally, the reported reduction in maximum voluntary isometric strength for the tibialis anterior (TA) muscle was ~40%, and the durations of the stimulated twitch properties were prolonged by as much as 50% in men over 80 yr compared with young men (20–32 yr) (46).

In conjunction with the observed age-related slowing of contractile properties, it is reasonable to expect that MU firing rates recorded during voluntary contractions will be matched appropriately in both old and young adults. However, there have been only a limited number of studies examining changes in firing rate with age, and the results are inconsistent. Comparisons are difficult between the few studies reported because a variety of methods and procedures have been used. For example, MU discharge rates at forces <20% maximum voluntary contraction (MVC) were studied in biceps brachii, triceps brachii, TA (26), and abductor digiti minimi (33, 41). These studies suggest a nil-to-moderate reduction in firing rate (0–33% lower) at forces <20% MVC normalized force in old adults (67–89 yr) compared with young adults (20–40 yr). Only two studies, one in small muscles of the hand (28) and one in an intrinsic foot muscle (7), have reported firing rate changes with age at voluntary force levels >20% MVC. Borg (7) reported that MU firing rates were similar in extensor digitorum brevis muscles from young and old (65–80 yr) subjects at 100% MVC. However, Kamen et al. (28) reported decreased MU firing rates with age (67–85 yr) in the first dorsal interosseus muscle at 100% MVC but, perhaps surprisingly, not at 50% MVC. Generally, the limited data suggest a trend toward a reduction in MU firing rates with age (for review see Ref. 38); however, no studies have measured average MU firing rates from a large number of MU trains in steady-state contractions ranging from low level to MVC in subjects aged 80 yr or older.

Contractile property changes with age have been reported in a variety of human muscles, but these quantitative and qualitative muscle characteristics have not been correlated systematically with MU firing rates in old humans. However, in young adults, Borg et al. (8) and Grimby et al. (23) studying extensor digitorum muscles concluded that faster axonal conduction velocities, representing the faster motoneurons, corresponded with higher MU discharge rates and shorter twitch contraction times. Bellemare et al. (4) reported a positive relationship between mean maximal MU firing rates and whole-muscle contractile speed when results from young adults were compared from three different muscles (biceps brachii, adductor pollicis, and soleus).
with varying contractile speeds. The soleus muscle had the slowest contractile speeds, the lowest overall MU firing rates, and the narrowest firing rate range at MVC compared with the adductor pollicis and biceps brachii muscles (4). More recently, at the level of an individual MU by using microelectrode techniques, Mackenzie et al. (30) found that the toe extensor MUs in young adults had slower contractile speeds and lower firing rates than did MUs recorded from the thenar muscles of the hand. These studies support the concept of matching (1) between parent motoneuron firing rates and their constituent muscle fiber contractile properties. Furthermore, compared with normal adults, lower relative firing rates with correspondingly slowed muscle contractile characteristics have been documented in patients with multiple sclerosis (36) and in stroke victims (18). Thus the purpose of this study was to match the contractile characteristics found in the young to those of the older adults and to determine whether the functional relationship between MU firing rate and muscle contractile speed was changed with age.

MATERIALS AND METHODS

Subjects. Six old men (age range 80–85 yr) and six young men (age range 20–22 yr) volunteered for the study. Subjects were comparable with respect to height, mass, and hours of recreational activity per week (Table 1). Participation in recreational physical activity was quantified for young and old subjects by using the Yale Physical Activity Survey for Older Adults (11). Recreational activities reported by the subjects included walking, golf, tennis, intramural basketball, and bicycling.

Exclusion criteria for subject participation in the study included known neurological or orthopedic pathologies of the lower limb, diabetes, alcoholism, recent bed rest >3 days, uncontrolled hypertension or angina, running >10 km/wk, or strength training of the ankle dorsiflexor or plantar flexor muscle groups. This information was obtained by review of a screening checklist and interview. The potential effects of caffeine on muscle properties (32) were controlled by requiring that subjects not consume caffeinated beverages for at least 2 h before the laboratory sessions. All subjects provided informed written consent according to the guidelines established by the University's Review Board for Health Sciences Research Involving Human Subjects.

Contractile property measurements. Subjects were seated with both the hip and knee joints positioned at an angle of 90° of flexion. The subject’s right foot was fixed in an isometric dynamometer at an angle of 30° of plantar flexion (46) with the ankle joint aligned at the axis of rotation of the footplate. Excessive lower extremity movement during ankle dorsiflexor contractions was prevented by immobilizing the subject’s right thigh with a seatbelt applied firmly across the hips, and the knee was secured in the dynamometer. Voluntary and electrically stimulated muscle torques were transmitted through a rigid footplate at a fixed distance (20 cm) from the strain gauge mounted at the joint axis of rotation (35). The output from the strain gauge was amplified and sampled on-line at 500 Hz. The strain gauge was calibrated with known weights to confirm a linear relationship between torque input (N·m) and voltage-output values. Muscle torque production was displayed on an oscilloscope during voluntary or stimulated muscle contractions for visual feedback to the subject.

To assess the contractile properties of the TA, both voluntary and electrically stimulated contractions were elicited. Electrical stimulation was delivered to the TA muscle through two commercially available carbon rubber electrodes (4.5 × 3.75 cm) secured to the right leg with Velcro straps. The cathode was fixed over the common peroneal nerve just below the head of the fibula, and the anode was fastened over the proximal half of the TA muscle just distal to the tuber tibiae (46). Stimulating electrode positions were modified slightly from subject to subject, for anatomic variation, to obtain the largest muscle twitch torque. The voltage of a 50-μs square-wave pulse (model 3072-134, Digitimer, Hertfordshire, UK) was increased incrementally up to 200 V. Maximum twitch torque was measured at the voltage level that activated as much of the TA muscle as possible without interference from antagonist muscles. Antagonist interference was noted as a decrease in twitch torque with continued increase in voltage. Potentially confounding ankle extensor muscle contraction was monitored during TA stimulation by visual inspection and palpation of the muscle tendon involvement. Maximum twitch tension corresponded to ~10% of the subject’s MVC torque. With the subject at rest, three separate trials of twitch responses were recorded by using a series of 10 single 50-μs square-wave pulses delivered at 1 pulse/s. Approximately 2 min of rest were given between each series of twitches.

Off-line quantification of the twitch response consisted of measures of peak twitch tension (P1), time to peak tension (TPT), and half relaxation time (RT1/2). TPT and RT1/2 were summed as a measure of twitch contraction duration (CD). Group means for TPT, RT1/2, CD, and P1 were calculated for all the analyzed twitches. Because subjects returned to the laboratory for several MU recording sessions (see Intramuscular MU electromyography (EMG)), twitches, MVC and interpolated twitch tests were repeated two to three times on each subject. Test-retest variability for all measures was <5%.

To evaluate the ability of the young and old subjects to activate their dorsiflexors during an MVC, a modified twitch interpolation test was used (21). For this test, a series of paired electrical shocks (2 pulses separated by 10 ms) were delivered once per second during a 4- to 5-s MVC and immediately after the MVC during rest (post-MVC). Visual feedback from the oscilloscope and strong verbal encouragement were given to the subject during the MVC. Three separate trials were performed with 5-min rest periods, and

| Table 1. Summary of subject characteristics by age group |
|----------------|----------------|----------------|
| Subject Characteristics | Young Men | Old Men |
| Age, yr | 20.8 ± 0.8 | 82.0 ± 1.7 |
| Height, cm | 179.5 ± 5.7 | 168 ± 5.8 |
| Mass, kg | 80.2 ± 6.5 | 77.7 ± 7.6 |
| Recreational activity, h/wk | 7.6 ± 2.3 | 6.7 ± 3.9 |
| Values are means ± SD with range in parentheses for 6 subjects in each group. |
the highest value from the three MVC trials was recorded as the subject's maximum voluntary torque for that test session. If an effort by a subject was not maximal during an MVC, the paired stimuli during the MVC elicited small twitch responses superimposed on the voluntary torque level. An amplified view of the torque record off-line was used to determine the size of any superimposed responses. Average superimposed twitch values were calculated for each subject as the mean of the torque of two to three interpolated twitches. Post-MVC twitch torques were the mean torque of three to four post-MVC twitch records at rest. A ratio of these two twitch torques provided an index of activation during an MVC trial [%activation = (1 − (superimposed twitch torque/post-MVC twitch torque)) × 100%].

In an effort to ensure that stimulated muscle contractile properties were not affected by temperature, skin surface temperature over TA was measured with a thermistor (Digital Thermometer, Yellow Springs Instruments, Yellow Springs, OH). Surface skin temperature was stable within and between test days with an average of 29.1 ± 1.2°C and a room temperature of 20−22°C.

Intramuscular MU electromyography (EMG). By using intramuscular EMG recording methods (5, 6, 36, 40), single MU firing rates were recorded during steady-state voluntary contractions varying in intensity from ~10 to 100% of subjects' MVCs. Intramuscular EMG recordings were obtained from the right TA muscle by using custom-made insulated tungsten microelectrodes (125 μm in diameter, 6 cm in length, 5-μm bared tips). Before insertion of the microelectrode through the skin, the skin surface over the TA muscle was cleansed thoroughly with 70% ethanol. To improve the number of different MUs sampled during each contraction, two microelectrodes (connected to separate channels) were inserted into the TA muscle, spaced ~4.5 cm apart. A common reference surface electrode for the two microelectrodes was fixed over the patella. Each microelectrode was slowly advanced (~0.5 cm/contraction) and manipulated independently by two operators so that recordings of potentials were made from as many different MUs as possible from various regions and depths of the muscle. After several contractions, the microelectrode was repositioned in the TA to maximize sampling of MUs from the different major TA compartments, which have been described by Wolfs and Kirk (48). A mathematical probability study in vastus lateralis in which this recording technique was used suggests that, although muscle fibers from different MUs are interspersed in a given region of a muscle, the probability of duplicate recordings of the same MU is low, at least for young adults (37). Furthermore, the authors concluded that the influence of any duplicate recordings on mean MU firing rate over the entire range of torque would be insignificant. During the contractions, identification of discrete series of action potentials (APs), which will be referred to as MU trains, was facilitated for the operators by using visual and audio feedback of the intramuscular recordings.

To acquire a large number of MU trains at various torque levels, and to avoid fatigue-related effects on MU firing rates (6), subjects attended five to seven laboratory sessions for repeated experiments over a period of 2 wk. During each visit, subjects performed a brief 5-s maximum dorsiflexor contraction (MVC) with the microelectrodes inserted in the TA muscle. This contraction torque was used as the subject's 100% MVC target value for the test session. Submaximal target torques (10, 25, 50, and 75% MVC) were marked on the oscilloscope, and subjects were asked to generate torque at the target levels. A series of 5- to 10-s isometric contractions at various torque levels (10–100% MVC) were conducted in randomized order. The lower intensity torque contractions (10 and 25% of MVC) were held for no more than 10 s, whereas the higher contractions were limited to 6 s in duration. Rest periods of 2–5 min were given between trials to minimize the effects of fatigue. For each contraction the subject was asked to generate torque to the target level as quickly as possible and to hold the target torque steady for the required time. During the rest periods, the straps confining the subject's foot were loosened occasionally to prevent ischemia and the potential effect of reduced muscle torque production secondary to restricted blood flow. The leg of the subject was in the device for up to 1 h during the recording of MU trains.

The two channels of intramuscular TA MU EMG were amplified (>100−10,000) and wide-band filtered (between 10 Hz and 10 kHz) by using a NeuroLog NL824 (Hertfordshire, UK) preamplifier, amplifier, and filter. After amplification and filtering, all signals from the two EMG channels were converted from analog-to-digital format by a 12-bit analog-to-digital converter (model 1401 Plus, Cambridge Electronic Design, Cambridge, UK). Intramuscular EMG recordings were sampled each at 12 kHz. Signals were monitored on the computer screen and oscilloscopes and collected on-line concurrently to a video cassette recorder.

Of-line analysis of raw intramuscular EMG data consisted of manually comparing individual APs from an identified MU train using a software window discriminator, shape recognition, and overlay of sequential APs (Spike2 software, Cambridge Electronic Design). An example of two identified MU trains is shown in Fig. 1. A minimum of five contiguous interspike intervals (i.e., 6 APs) was required for firing rate analysis of a MU train. In addition to shape recognition of APs from six contiguous spike discharges, interspike interval discharge variability also was used as an independent, and often final, criterion in the classification of APs from one MU. This criterion is useful especially at high force levels (75 and 100% MVC) when many units are recorded by the electrode at high firing rates and often with the minimum number of intervals available for rate calculation. Discharge variability was calculated as the coefficient of variation (CV), such that the SD of the MU firing rate (Hz) was divided by the mean firing rate to obtain a measurement of variability that was normalized to 100% CV (%) = [SD (Hz)/mean firing rate (Hz)] × 100%. Studies have shown (see Ref. 19) that discharge variability can be as high as 30%, and thus we chose no higher than 30% CV for acceptance of a MU train in combination with the main criteria outlined above. Studies to date are equivocal on whether discharge rate variability differs with age (38). Although very labor intensive, these methods minimized the possibility of falsely classifying APs from two or more MUs as arising from one MU. To ensure consistency in interpretation, all MU trains were analyzed by one individual.

Data reduction and statistics. MU firing rate data collected during voluntary contractions were categorized according to the torque ranges into five classification bins. Voluntary torque values across all target torque levels were normalized to the highest maximum torque produced by the subject in that test session with microelectrodes inserted. For statistical analysis, normalized voluntary torque ranges were used to categorize subjects' intramuscular EMG data into five classification bins: a 10% bin contained torque levels ≤12.5% MVC, a 25% bin contained >12.5 to ≤37.5% MVC, a 50% bin contained >37.5 to ≤62.5% MVC, a 75% bin contained >62.5 to ≤87.5% MVC, and a 100% bin contained >87.5 to 100% MVC.
Age-related differences in MVC torque and percent activation were analyzed with unpaired Student's t-tests. Twitch contractile property data (P₀, TPT, RT₁/₂, CD) were found not to be normally distributed by statistical analysis and were analyzed with Mann-Whitney rank-sum tests. Age group differences in MU firing rate at voluntary torque levels of 10, 25, 50, 75, and 100% of MVC were analyzed independently with two-way repeated-measures analysis of variance, by using age and voluntary torque level as factors for statistical comparison. Tukey post hoc tests were used to identify differences when statistically significant interactions were found between the two factors of age and voluntary torque level. Regression analyses were performed to determine the relationship between torque and MU firing rate for the young and the old subjects by using raw data MU trains. Pearson correlation coefficient (r) relationships were calculated between subjects’ MU firing rates and twitch contractile properties. Values for all group data are indicated as means ± SD. The critical value for statistical significance was set at P < 0.05 for all tests.

RESULTS

Voluntary and electrically stimulated torque recording. The results from measurements of torque production and contractile properties of TA muscle from young and old subjects are presented in Table 2. Mean dorsiflexor MVC torque was 26% lower (P < 0.01) for the old group compared with the young (Table 2). MVC torque with inserted microelectrodes varied ~8% daily, and MVC torque with inserted microelectrodes varied ~7% daily from MVCs without inserted microelectrodes. During MVCs, electrically stimulated superimposed paired stimuli demonstrated that the TA muscle of the young and old subjects could be activated equally by voluntary effort (99.3 and 99.1%, respectively). Muscle twitch contractile speed properties (TPT, RT₁/₂, CD) were all statistically different between young and old subjects. Old subjects had 19% longer TPT, 28% longer RT₁/₂, and 25% longer CD (CD was calculated to be the
sum of TPT and RT_{1/2} durations) than did the young subjects (Table 2). No difference was observed between Pt in young and old subjects (Table 2).

Intramuscular needle EMG. With use of the combination of criteria outlined in MATERIALS AND METHODS, a total of 1,902 MU trains was identified manually (965 from the old subject group and 937 from the young subjects) (Fig. 2). The higher force contractions are the most difficult for identifying discrete MU trains. For each force level the number of units identified was similar in each age group. The total number was 1,750 MU s at MVC, 450 at 75% MVC, 450 at 50% MVC, 700 at 25% MVC, and 750 at 10% MVC. Figure 2 is a scatterplot relating TA MU firing rates (Hz) with isometric dorsi-flexor torque production (%MVC). Each raw data set of MU trains was fit with a linear regression line to compare the relationship between MU firing rate and voluntary torque level for the young and old men. Similar and parallel relationships were found between age groups, indicating that the motoneuron pool firing rates were similarly lowered across all torque levels; however, the relationship between MU firing rate and torque production was maintained with aging. Group means of binned MU firing rates (Hz) (bin classification as described in MATERIALS AND METHODS) at each of 10, 25, 50, 75, and 100% MVC torque levels were significantly lower for old subjects compared with young subjects [F(1,4) = 41.8, P = 0.002].

Table 2. Tibialis anterior contractile properties in young and old men

<table>
<thead>
<tr>
<th>Muscle Property</th>
<th>Young Men</th>
<th>Old Men</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to peak tension, ms</td>
<td>98.5 ± 6.9</td>
<td>116.9 ± 8.0*</td>
</tr>
<tr>
<td>Half relaxation time, ms</td>
<td>86.5 ± 7.0</td>
<td>110.7 ± 9.0*</td>
</tr>
<tr>
<td>Contraction duration, ms</td>
<td>184.9 ± 7.9</td>
<td>231.6 ± 12.2*</td>
</tr>
<tr>
<td>Peak twitch tension, N·m</td>
<td>3.1 ± 0.4</td>
<td>3.0 ± 1.0</td>
</tr>
<tr>
<td>Maximal voluntary contraction, N·m</td>
<td>44.2 ± 5.1</td>
<td>32.6 ± 5.3*</td>
</tr>
<tr>
<td>%Activation</td>
<td>99.3 ± 0.1</td>
<td>99.1 ± 0.2</td>
</tr>
</tbody>
</table>

Values are means ± SD with range in parentheses for 6 subjects in each group. *P < 0.01.

Fig. 3. Binned MU firing rates plotted against normalized torque for both age groups. ●, Young subjects; ○, old subjects. Axes are reversed from Fig. 3 to be consistent with usual method of plotting stimulated tension-frequency curves. Values are means ± SD. *Group mean MU firing rates across all relative torque levels were significantly lower for old subjects compared with young subjects [F(1,4) = 41.8, P = 0.002].

Fig. 2. Scatterplot of normalized torque level against MU firing rate for 1,902 AP trains. Similar number of data points were plotted for both age groups: 965 from old subjects and 937 from young subjects. Young subjects; ○, old subjects. Linear regression equations for raw data sets are as follows: frequency_{(Hz)} (young) = 0.30 × force_{(N·m)} + 8.44, \( r^2 = 0.65 \) (top line); and frequency_{(Hz)} (old) = 0.27 × force_{(N·m)} + 4.18, \( r^2 = 0.62 \) (bottom line).
old subjects. Similar relative torques were achieved with lower mean MU firing rates in the old subjects. For example, at 50% MVC, the mean firing rate was \(\sim 14\) Hz for the old subjects compared with \(\sim 23\) Hz for the young subjects. This 9-Hz difference is functionally significant because a rate of 14 Hz in the young subjects would only generate \(\sim 25\%\) MVC. An increase of only \(\sim 6\) Hz in mean MU discharge rate was required to attain 50% MVC torque level in the old group from the mean MU firing rate at 10% MVC. In comparison, the mean firing rates in young subjects were increased \(\sim 10\) Hz between 10 and 50% MVC. The \(\sim 4\)-Hz difference in discharge rate between the age groups, at the steepest portion of the curve, represents 18% of the total firing rate range (\(\sim 22\) Hz) available to old subjects (a range of \(\sim 22\) Hz was found between the mean firing rate \(\sim 9\) Hz at 10% MVC and the mean \(\sim 31\) Hz at 100% MVC).

Firing rates were normally distributed in both groups at each torque level. The histogram distribution of MU firing rates across all target torque levels reflects the range of firing frequencies originating in the motoneuron pool (6). MU firing rates from all five target torque levels were plotted to create histograms for each subject group (Fig. 4). The overall range of firing rates was similar for young and old subject groups.

Firing rate-CD relationships. The \(r\) values were relatively more similar and stronger at the lower torque levels than at the 100% MVC level; the correlations across the three torque levels ranged from moderate \((r = -0.67)\) to good \((r = -0.84)\) (10) (Fig. 5). To determine the relationship between firing rate and muscle contractile properties, individual subject mean firing rates from low (10%), moderate (50%), and maximal torque (100% MVC) levels were correlated with the subject's corresponding mean twitch CD. When plotted, clear groupings of data were evident, and young and old subject CD data points did not overlap. In addition, the firing rate-CD plot spans a broad and representative continuum of muscle CDs (minimum 179.7 ms, maximum 246.6 ms) and MU discharge rates (minimum 8 Hz, maximum 47 Hz).

**DISCUSSION**

The isometric contractile properties of TA in the old men illustrate the characteristics of “aged muscle,” namely, a reduced torque output and slower contractile properties compared with those of young adults. In addition, old men were able to activate the TA muscle to a similar high level (99%) as were the young men; however, their mean maximal torque level was only 74% of that produced by the young men. These age-related findings of a slower and weaker muscle with no difference in ability to voluntarily activate the dorsiflexors have been reported in previous studies of TA and other limb muscles (3, 46, 47). Although several studies have described MU firing rates for TA in young adults at a variety of voluntary torque levels, including MVC, none have reported firing rates for subjects aged 80–85 yr or compared the rates with the whole muscle contractile properties for either age group. The results from over 900 MUs in each age group showed that mean MU firing rates in TA of healthy, active old men were significantly lower at all relative torque levels (10, 25, 50, 75, and 100% MVC) compared with those from young men (20–22 yr). The reduction in firing rate with age seems to parallel the weaker and slower contracting muscle and provides indirect support for the concept of age-related neuromuscular remodeling, at least for the TA muscle.

**Voluntary and electrically stimulated torque recording.** Contractile properties of TPT and RT\(_{1/2}\) were significantly longer, 19 and 28% respectively, in muscle of old vs. young subjects. The data for the old subjects were in general agreement with those in previous
MOTOR UNIT FIRING RATES IN AGED HUMANS

Fig. 5. Pearson correlation coefficient (r) relationships between individual muscle contraction durations (CD) and subjects’ MU discharge rates collected at 3 torque levels are plotted for MVC, 50% MVC, and 10% MVC. □, ○, △, young subjects; ■, ●, ▲, old subjects. Relationships between the variables ranged from moderate (r = 0.67) to good (r = 0.84). TPT, time to peak tension; RT 1/2, half relaxation time.

Intramuscular needle EMG. At all relative torque levels the old subjects had significantly lower mean MU firing rates (30–35% reduction) compared with the young subjects, and, as steady-state torque increased, mean firing rates increased near linearly and to a similar relative degree in both groups. The torque-firing frequency relationship plot for the old men has a lower y-intercept, but the slope of the relationship is similar to that of the young men (Fig. 3). The similar slopes of this relationship between the two groups suggest that age has not changed the strategy used by the central nervous system to grade muscle torque (40) but that the firing rates simply are lower by the same amount at all torque levels tested. The minimum and maximum MU firing rates, for any subject within an age group from all the recorded voluntary contractions, were ~7 Hz at 10% MVC and ~65 Hz at 100% MVC for the young subjects and were ~5 Hz at 10% MVC and ~62 Hz at 100% MVC for the old subjects (Fig. 4). Thus the range of MU firing rates collected was similar for the young and old subjects; however, the lower mean MU firing rates in TA muscles of the old subjects suggest that there are significantly fewer fast-firing MUs contributing to the mean discharge rates.

Previous studies of TA firing rates have reported firing rates either at forces of >50% MVC in young adults or at low-level threshold forces (~1% MVC) in old adults. In the present study, the mean MU discharge rate at 100% MVC for the young subjects was 41.9 ± 8.2 Hz; 6% of the total number of MU trains collected had discharge rates >45 Hz. Bigland-Ritchie et al. (5) found mean TA MU firing rates in young subjects of 32.1 ± 10.7 Hz at 100% MVC and reported that ~5% of the total number of trains collected at MVC were at rates >45 Hz. The higher mean MU firing rate at 100% MVC in the present study, compared with that of the study of Bigland-Ritchie et al., may be explained by our larger sample of MU trains and, because age-related neuromuscular slowing of TA begins as early as the fifth decade in humans (46), perhaps because of the younger age (~15 yr) of the subjects in this study. Van Cutsem et al. (44) reported maximal firing rates in young adults of 33.2 ± 14.7 Hz, and Grimby et al. (24) found rates of ~60 Hz during brief maximal voluntary bursts in TA muscle of young subjects but did not report average firing rates during steady-state contractions. Van Cutsem et al. (44) employed ramped voluntary contractions of ~10-s duration and collected maximal MU discharge rates as the subject attained MVC at the end of the ramped contraction. The prolonged length of the contractions in the Van Cutsem et al. study may have induced fatigue resulting in lower maximal MU firing rates at MVC (see Ref. 6) compared with those from this study in which contraction length, particularly at torques above 25% MVC, was <6 s in duration.

Submaximal torque level MU firing rates previously reported for young subjects were within 1 SD of the mean discharge rates recorded from muscles of the young subject group. Bigland-Ritchie et al. (5) reported mean MU firing rates of 17 and 23 Hz at 50 and 75% MVC, respectively. The mean MU firing rates recorded in muscles of our young subjects were 22 ± 6.3 and 28 ± 7.8 Hz at 50 and 75% MVC, respectively. Although Bigland-Ritchie et al. did not report firing rates at 10 and 25% of MVC, the range of firing rates at the higher torque levels, from 50 to 100% MVC, was comparable to our results. At the lowest submaximal level (10% MVC) in young adults, we found a mean firing rate of 12.2 ± 2.4 Hz. Only one other study (26) has reported low-torque-level firing rates for TA of young adults (20–40 yr): 8.0 ± 0.9 Hz recorded at threshold (~1% of MVC). After a linear regression was fitted through the MU firing rate-torque scatterplot in Fig. 2, extrapolated threshold firing rates for our young subjects would be ~8 Hz. The only reported MU firing rate in TA of old
subjects (61–80 yr) was 7.6 ± 1.1 Hz at threshold force (26). A linear regression fit of the MU scatterplot for the old subjects in Fig. 2 would predict threshold rates in our study to be near 5 Hz.

Firing rate-CD relationships. The relationships between steady-state torques and MU firing rates has not been reported previously for the TA muscle in either young or old men. In addition, few studies have discussed the relationship between the motoneuron firing rate and its muscle unit contractile properties in humans (4, 36). Previous studies of human extensor digitorum brevis muscle found that during voluntary contractions MUs firing at low frequencies (<10 Hz) had slow axonal conduction velocities (30 and 35 m/s) and MUs firing mainly in high-frequency bursts had fast axonal conduction velocities (40 and 54 m/s) (8). Grimby et al. (23) found that extensor digitorum brevis MUs, which were driven continuously at low firing rates of 10–30 Hz, had slow twitch contraction times between 60 and 90 ms, whereas MUs firing in bursts at 20–40 Hz had shorter twitch contraction times between 40 and 55 ms. The combination of the results of these two studies suggests that axonal conduction velocities are related to MU firing rates, and these properties are correlated with muscle twitch CDs.

In the present study, motoneuron firing rate and muscle twitch contractile speed were negatively related in the neuromuscular systems of young and old men. MU firing rates were higher for muscles with shorter CDs in young subjects, and lower MU firing rates were correlated with longer muscle CDs in old subjects. The concept of matching between the motoneuron cell and the muscle fibers it innervates was first described when Eccles et al. (15) found a positive correlation between muscle twitch CD and motoneuronal postspike afterhyperpolarization (AHP) in animals. Bakels and Kernell (1) and Gardiner and Kernell (22) have published a series of papers exploring the relationship between individual muscle fiber contractile properties and their spinal motoneuron firing rate in reduced animal preparations. These studies yielded evidence that muscles with slower twitch CDs also had correspondingly longer spinal cell AHPs. These studies indicate also that to a large degree AHP determines spinal motoneuron firing rates. Furthermore, Englehardt et al. (16) have shown that AHP is longer in spinal motoneurons in aged rats. Thus, by using the aging human model, our population sampling of motoneuron firing rates compared with whole-muscle CDs provides indirect support for this matching principle.

Age-related remodeling. There is substantial evidence from several preparations for age-related remodeling in the neuromuscular system. Slowed contractile properties, higher innervation ratios of slow-twitch MUs, and reduced fiber number and size with aging in humans (9, 12, 20, 34) and rats (27) all have been well documented. In addition, the loss of MUs and a reduction in various electrical properties with age in humans have been reported (13). For example, reduced MU firing rates in a hand muscle (first dorsal interosseous) were found only at 100% MVC, but not at a submaximal level (50% MVC) in old compared with young adults (28). However, Howard et al. (26) reported that submaximal firing rates (10% MVC) in the TA muscle of old subjects were significantly reduced in comparison to young subjects. In the present study, at all steady-state torque levels tested in the TA, mean MU firing rates were substantially reduced in men who were ~60 yr older than in the young men. In addition, we have confirmed that with age the dorsiflexors, of which the TA is the greatest contributor (31), become weaker and slower contracting. Histochemical studies have shown that in young adults the TA contains 70–75% type I fibers, whereas this is increased to 85% type I fibers in older adults (48). Taken together, these findings suggest that overall a slower motoneuron pool exists for the TA of old subjects, which indirectly supports the age-related remodeling process theory. However, the remodeling process is not complete because some MUs with high discharge rates were still found in TA muscle of the old men.

The functional implication for the coordinated slowing of the electrical and mechanical muscle properties in the muscle of the old subjects is that fused tetanus of the slower muscle would be achieved at reduced MU firing rates. Stimulated tetanic fusion frequency is lower with slower muscle contractile speed (6, 20), and, similarly, during voluntary contractions longer relaxation rates in muscles of old subjects would attain muscle tetanus at lower steady-state motoneuron discharge rates. Firing rates in excess of those required to maintain tetanic tension would be ineffective for further torque production. The leftward shift in the torque-firing frequency curve of the old subjects in relation to the young subjects in this study (Fig. 3) suggests that lower firing rates were used to attain the same relative torque output (%MVC). On the basis of the remodeling theory, it is likely that the contractile properties of the remaining and reinnervated MUs in aged muscle reflect the influence from new and different motoneuron discharge rates. However, an alternate hypothesis is that aging could affect muscle fibers independent of their parent motoneurons (see Ref. 2), whereby changes in muscle properties influence the motoneurons such that an appropriate match between firing rates and contractile speed is maintained.

Possible mechanisms for age-related reductions in motoneuron firing rates. The lower MU firing rates of the TA muscle in old subjects simply may be due to larger MUs in the elderly, innervated primarily by slow motoneurons as based on previous histological, biochemical, and electrophysiological muscle evidence (13, 38). In addition, MU firing rates may be reduced by the following: 1) age-related limitations in excitability of the corticospinal tract (39) and of the motoneurons (16); 2) increased duration of the motoneuron AHP, which would impose an upper limit on maximum MU discharge rates (16); 3) reductions in the maximum conduction velocity, or slowing of motor nerve fiber signal propagation with aging, which has been reported for upper and lower extremity motor nerves in humans (9, 13); and 4) muscle fiber disuse from short-term
immobilization, which showed decreased maximal firing rates in hand muscle (14).

It is interesting to note that the old subjects in this study are unlikely to be representative of the overall population of humans in their ninth decade of life. They represent a group who have aged well and are relatively healthy and active. In fact, their activity profile (Table 1) was similar to the young men in recreational activity hours per week. Even though the changes reported in the present study are substantial with regard to weakness, slowing and lower MU firing rates, it is tempting to speculate that men in poorer health and who are less active might show even greater age-related reductions in these MU and muscle properties. Whether the changes in TA MU properties at a variety of torque levels with age are similar for other human limb muscles is not known. Also, other studies have not compared firing rate property findings with contractile properties. Most of the limited work on age-related changes in firing rates has concentrated on hand muscles with variable findings (38). Thus muscles of the upper limb, muscles of varying fiber type composition, and muscles specialized for fine tasks vs. postural control all may be affected differently with age.

We thank Dr. Sharyn Vanden Noven for useful comments on an earlier version of this manuscript.

This study was supported by the Natural Sciences and Engineering Research Council of Canada and the Royal Canadian Legion in conjunction with the Physiotherapy Foundation of Canada.

Address for reprint requests and other correspondence: C. L. Rice, Center for Activity and Ageing, St. Joseph’s Health Center Annex, 1490 Richmond St., London, ON, Canada N6G 2M3.

Received 10 August 1998; accepted in final form 13 April 1999.

REFERENCES


