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Triceps surae contractile properties and firing rates in the soleus of young and old men

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Dalton BH, Harwood B, Davidson AW, Rice CL. Triceps surae contractile properties and firing rates in the soleus of young and old men. *J Appl Physiol* 107: 1781–1788, 2009. First published October 1, 2009; doi:10.1152/japplphysiol.00464.2009.—Mean maximal motor unit firing rates (MUFRs) of the human soleus are lower (5–20 Hz) than other limb muscles (20–50 Hz) during brief sustained contractions. With healthy adult aging, maximal MUFRs are 20–40% lower and twitch contractile speed of lower limb muscles are 10–40% slower compared with young adults. However, it is unknown whether the inherently low maximal MUFRs for the soleus are further reduced with aging in association with age-related slowing in contractile properties. The purpose of the present study was to compare the changes in triceps surae contractile properties and MUFRs of the soleus throughout a variety of contraction intensities in six old (~75 yr old) and six young (~24 yr old) men. Neuromuscular measures were collected from the soleus and triceps surae during repeated sessions (2–6 sessions). Populations of single MUFR trains were recorded from the soleus with tungsten microelectrodes during separate sustained 6- to 10-s isometric contractions of varying intensities [25%, 50%, 75%, and 100% maximal voluntary isometric contraction (MVC)]. The old men had weaker triceps surae strength (MVC; 35% lower) and slower contractile properties (contraction duration; 20% longer) than the young men. However, there was no difference in average MUFRs of the soleus at 75% and 100% MVC (~14.5 Hz and ~16.5 Hz, respectively). At 25% and 50% MVC, average rates were 10% and 20% lower in the old men compared with young, respectively. Despite a significant slowing in triceps surae contraction duration, there was no age-related change in MUFRs recorded at high contractile intensities in the soleus. Thus the relationship between the whole muscle contractile properties and MUFRs found in other muscle groups may not exist between the triceps surae and soleus and may be muscle dependent.

aging; electromyography; isometric strength; motor unit

THE AGING PROCESS is associated with a loss in muscle mass, termed sarcopenia, that is accompanied by losses in strength and power (40). There are several contributing factors within the neuromuscular system that have been implicated in sarcopenia (for reviews, see Refs. 1, 19, 44), including changes in the structure and function of motor units (MUs) (25). It is often accepted that MU firing rates (MUFRs) are reduced with aging, but when results from the relatively few studies are compared, this general conclusion needs to be qualified in relation to contraction intensity and muscle group (40). For example, MUFRs were similar between old and young men for the vastus medialis at any contraction intensity (41) and for many other appendicular muscles at low [<50% maximal voluntary isometric contraction (MVC)] contraction intensities (42). However, for the first dorsal interosseous (12, 21), abductor digiti minimi (38), tibialis anterior (4, 37), and the vastus lateralis (20), rates were found to be 20–64% lower in the old compared with young men at contraction intensities of 50% MVC or greater.

Studies using animal and human preparations suggest that whole muscle contractile properties are matched to motoneuron discharge rates to achieve optimal force generation (3, 23). Usually muscles from aged animals and humans have slower contractile properties compared with younger adults (28, 40), but surprisingly, in humans, few studies have compared those age-related changes in contractile properties with changes in MUFRs (4, 41). Previous reports have suggested that the relationship between firing rates and contractile properties established in young adults across muscle groups (3) is maintained with aging (4, 21). In one study of the tibialis anterior (4), when old and young men were compared, slower isometric contractile properties were related to lower mean MUFRs recorded at submaximal and maximal contraction intensities. In one other study of the vastus medialis, contractile properties were marginally (<10%) slowed with age, and MUFRs were not significantly lower in the old compared with young adults (41). Although not conclusive, these studies may indicate that a functional relationship between MUFRs and contractile speed is unaltered by aging. However, further studies are required to validate these observations and to help determine whether this is a fundamental principle of the neuromuscular system that is maintained with aging. To explore this question, we have chosen to study the soleus muscle.

The soleus is a unique model in that as part of the triceps surae complex this muscle has slow contractile properties compared with most other human limb muscles (3, 58) but is slowed further with aging (58). Typical contraction durations [CD; CD = time to peak twitch torque (TPT) + half relaxation time (HRT)] for the triceps surae group range from 188 to 253 ms in young men to 222 to 311 ms in men over 70 yr of age (53, 58). Additionally, one study (3) reported very low mean maximal MUFRs in the soleus (10.7 Hz) of young adults compared with mean rates for other limb muscles of 20–50 Hz, and they suggested that the low rates of the soleus matched its slowed contractile response. The interesting question here using the aging model is whether a muscle with very low maximal MUFRs will have even lower rates of discharge that will match the presumed age-related slower contractile properties. Unlike most other limb muscles, the soleus is rather homogeneous, being composed of >80% type I muscle fibers (18, 56), and although it does exhibit age-related contractile slowing, its mass (34) and estimated number of MUs (7) seem relatively well preserved with aging compared with other limb

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muscles (31, 34). Thus the purposes of the present study were *1*) to record comprehensively the mean steady-state firing rates of soleus MUs from low to maximal intensity contractions in old and young subjects, and *2*) to compare MUFRs with whole muscle contractile properties of the triceps surae. We hypothesized that because the soleus in some aspects is well preserved with aging and that skeletal muscles require some rate coding range to control force output effectively, the MUFRs recorded at high contraction intensities (>50% MVC) would not exhibit an age-related decrease to the same extent as those observed for other limb muscles. Because we expect age-related contractile slowing, this will result in a dissociation in the relationship between MUFR and contractile speed found in young adults.

MATERIALS AND METHODS

Subjects. Six old men (75.3 ± 4.1 yr old) and six young men (23.5 ± 2.9 yr old) volunteered for the study. Both the old and young groups were similar in height and weight (177.0 ± 4.2 cm and 88.0 ± 12.2 kg, and 173.7 ± 8.5 cm and 82.3 ± 11.8 kg, respectively). The old men were recruited from a local recreation program designed to maintain muscular endurance, cardiovascular fitness, and flexibility, whereas the young men were recruited from the university population. All participants were considered healthy, recreationally active, and free of neuromuscular disease. All old men had normal strength, reflexes, and sensation in the lower limbs with no clinical features of focal or generalized neuropathy. All participants granted oral and written consent before the testing. The local University's Review Board for Health Sciences Research Involving Human Subjects approved the study.

Experimental arrangement. Subjects were seated in an upright position in a custom-built isometric dynamometer (45) used to record plantar flexion torque. All tests were conducted on the dominant (right) leg with the hip, knee, and ankle angle positioned at 90°. Although the soleus contributes 70% of the triceps surae torque in an extended knee position (13), to further maximize its contribution the knee was flexed to 90° thus limiting torque contribution from the gastrocnemeii (5, 45). A C-clamp pressing against the distal aspect of the right thigh minimized extraneous leg and hip movement during the plantar flexion contractions. Two Velcro straps attached to the dynamometer footplate were fastened across the dorsum and the toes to secure the foot to the dynamometer footplate. Voluntary and electrically evoked plantar flexion torques were transmitted through a rigid footplate and strain gauge mounted at the joint axis of rotation. The strain-gauge output was sampled online at 500 Hz. Torque production was displayed on a computer screen for visual feedback. All electrically stimulated properties were evoked via stimulation of the tibial nerve at the popliteal fossa using a digitimer stimulator (Model DS7AH; Digitimer, Welwyn Garden City, UK) with a 100-μs square-wave pulse delivered at 400 V. Current output at these settings was adjusted to achieve supramaximal stimulation (see *Experimental procedures*).

Surface electromyography (EMG) signals and compound muscle action potentials (M-waves) were recorded with self-adhering pediatric electrocardiogram cloth electrodes (H59P Repositionable Monitoring Electrodes; Kendall, Mansfield, MA). Before placement of the surface EMG electrodes and insertion of the two microelectrodes, the skin locations were cleaned with 70% isopropyl alcohol. Recordings were made from the soleus and medial gastrocnemius muscle portions using a bipolar set-up with an interelectrode distance of ~2 cm. For the medial gastrocnemius the electrodes were placed over the muscle belly, whereas the soleus recording electrodes were placed ~2 cm distal to the border of the gastrocnemius in line with the midline of the soleus. A ground electrode was positioned over the lateral malleolus. Surface EMG signals were preamplified (×100), amplified (×2), and sampled on-line at 2,000 Hz.

Single MUFRs were recorded utilizing intramuscular EMG methods previously described (3, 4). Intramuscular EMG recordings were obtained with custom-made insulated tungsten microelectrodes (125 μm in diameter, 3–6 cm length, 5-μm bared tip). The benefit of this technique is to sample from many MUs from each subject presumably representing an overall MU profile per subject at all contraction intensities including 100% MVC. With careful analysis (see *Data analysis*) despite small electrode movements this method has shown that active MU trains can be identified for short contractile durations (1–5 s). The inherent limitation is not being able to follow recruitment and derecruitment of individual MUs at high contractile intensities. Those techniques that can follow units throughout the full range of contractile intensities often have a very low yield, and thus there is a technical compromise among these techniques.

Before testing, microelectrodes were sterilized in an autoclave (Napco model 9000-D Autoclave/Dryer; Precision Scientific, Chicago, IL) for ~45 min at ~130°. Two sterile microelectrodes (connected to separate channels) were inserted into the medial and lateral aspects of the soleus. A common reference surface electrode was placed over the anterior border of the tibia, and a ground was positioned over the medial malleolus. To ensure collection of as many MUs as possible from varying depths and regions of the soleus, each microelectrode was manipulated by a separate operator, and during each contraction was advanced slowly (<0.5 cm per contraction). The recording of discrete series of action potentials or MU trains was facilitated by visual (computer screen) and audio (audio speaker and headphones) feedback. After several contractions, the microelectrodes were repositioned to obtain recordings from different portions of the soleus. All intramuscular EMG signals were preamplified (×100) and bandwidth filtered (10 Hz to 10 kHz) using a Neurolog NL824 (Hertfordshire, UK) preamplifier and filter. Intramuscular EMG signals were sampled on-line at 12 kHz for each channel. All EMG channels were converted from analog-to-digital by a 12-bit analog-to-digital converter (model 1401 plus, Cambridge Electronic Design, Cambridge, UK).

Experimental procedures. During multiple visits (2–6 sessions) each separated by at least 7 days, torque and EMG data were collected. To find the maximum M-wave and corresponding twitch, the intensity (250–600 mA) of the stimulator was progressively increased until a plateau was achieved in the M-wave amplitude. Following the plateau in M-wave amplitude, the current was increased further by 10–15% to ensure complete activation of all motor axons. Before determining maximal voluntary torque, the two microelectrodes were inserted into the soleus. Three MVCs, each of ~7 s, were attempted, and all voluntary efforts were separated by at least 2 min of rest. MVC torque was taken as the highest torque value achieved from any of the three attempts. A supramaximal twitch was delivered during the peak plateau (Ts) and ~1 s following (Tr) each MVC. Voluntary activation of the triceps surae was assessed by the interpolated twitch technique {%activation = [1 − (Ts/Tr)] × 100} (54). An average of the peak voluntary activation, MVC strength, and whole muscle contractile properties for all sessions was used to calculate individual values. These measures have been shown to be reproducible from day to day in this muscle group (54). All subjects were well practiced with these procedures and were provided visual feedback and strong verbal encouragement during the MVC attempts.

Next, intramuscular recordings were collected during submaximal sustained isometric contractions at 25% and 50% MVC. Subjects were instructed to increase torque within 1–2 s up to the appropriate target line, outlined on a computer monitor, and hold the contraction for ~10 s as steady as possible. Subjects alternated attempts at each target torque until a total of three contractions at each intensity was completed. One final 10-s contraction was made at 75% MVC.

Data analysis, reduction, and statistics. Off-line analysis of the raw intramuscular EMG signal has been previously described (4, 41). The analysis consisted of manual comparison of individual action potentials from an identified MU train using a software window discriminator, shape recognition, and overlay of sequential action potentials (Spike 2, Cambridge Electronic Design). Although software facilitated the inspection and collation of potential sequential action potentials and was used to calculate rates and other statistics the ultimate comparison of the shape and amplitude of the individual action potentials deemed to represent a single train from one MU was performed visually by an experienced operator. Examples of two MU action potential trains extracted during an MVC are highlighted in Fig. 1. A minimum of four contiguous interspike intervals (i.e., 5 action potentials) was required for analysis of firing rate for each MU train. Additionally, all acceptable trains had a coefficient of variability (CV) of rate within the train of ≤30% and doublet discharges (≤10 ms) were not included. MUFR trains identified from the voluntary sustained isometric contractions were classified into one of four bins based on percentage of MVC. A 25% bin (>18% to ≤29% MVC), a 50% bin (>44% to ≤55% MVC), a 75% bin (>65% to ≤80%), and a 100% bin (>80% to 100% MVC). Torque values during the collection of single MU action potential trains were normalized to the peak MVC torque value recorded for that session. For surface EMG, a 1-s epoch was taken around the center of each submaximal contraction and the root mean square (RMS) was calculated for the submaximal contractions for the soleus and medial gastrocnemius and normalized to the RMS of the M-wave.

All data were analyzed using SPSS version 15 (SPSS, Chicago, IL). Subject, torque data, twitch characteristics, and mean slope and intercept of the regression analyses between torque and contraction intensity were analyzed using an unpaired *t*-test. A Mann-Whitney *U*-test was used to analyze voluntary activation between groups. A two-way ANOVA (age × contraction intensity) with repeated measures was used to analyze all other data. The level of significance was set at $P < 0.05$. If a significant main effect or interaction was present, unpaired *t*-tests were performed with a Bonferonni correction factor to determine where the differences existed. Regression analyses (R^2) were used to determine relationships between contraction intensity and MUFRs for both groups and subjects' MUFRs and contraction durations. Pearson correlation coefficients (*r*) were also calculated for subjects' contractile properties and MUFRs. Descriptive statistics in both text and figures are provided as means (SD).

RESULTS

Strength, voluntary activation, and contractile properties. The old men exhibited 35% weaker plantar flexion strength ($P < 0.05$) than the young men (Table 1). Despite weaker voluntary strength, both groups were equally capable of targeting the various torque levels [24.8 (SD 0.7)%, 49.4 (SD 0.7)%, and 74.0 (SD 0.7)% for the old; and 24.7 (SD 0.4)%, 49.7 (SD 0.5)%, and 73.3 (SD 1.3)% for the young]. Voluntary activation, as assessed by the interpolated twitch technique, was similar (>99%) in both age groups (Table 1; $P = 0.69$). Evoked peak twitch torques tended to be 30% lower ($P = 0.08$) in the old men compared with the young (Table 1). Measures of twitch contractile speed indicated a nonsignificant ($P = 0.11$) lengthening of the HRT (14%) for the old men, but a significant ($P < 0.01$) lengthening of TPT by 25% compared with the young men. Thus CD (TPT + HRT) was longer ($P < 0.01$) by 20% for the old compared with the young men (Table 1). The normalized maximal rate of relaxation (MRR) and maximal rate of torque development (MRTD) of the twitch (s^{-1}) were calculated by dividing the peak rate of change of torque (N·m/s) by the peak torque of the twitch (N·m). Maximal relaxation rate was not significantly slower ($P = 0.3$) in the old compared with younger men [−8.4 (SD 1.7) s^{-1} and −9.3 (SD 1.6) s^{-1}, respectively], but maximal rate of torque development was slower ($P < 0.05$) in the old than young men [13.4 (SD 1.1) s^{-1} and 15.6 (SD 1.4) s^{-1}, respectively].

Motor unit properties. The soleus M-wave peak-to-peak amplitude was 49% lower ($P < 0.01$) in the old men compared with young (Table 2). For the voluntary contractions at sub-

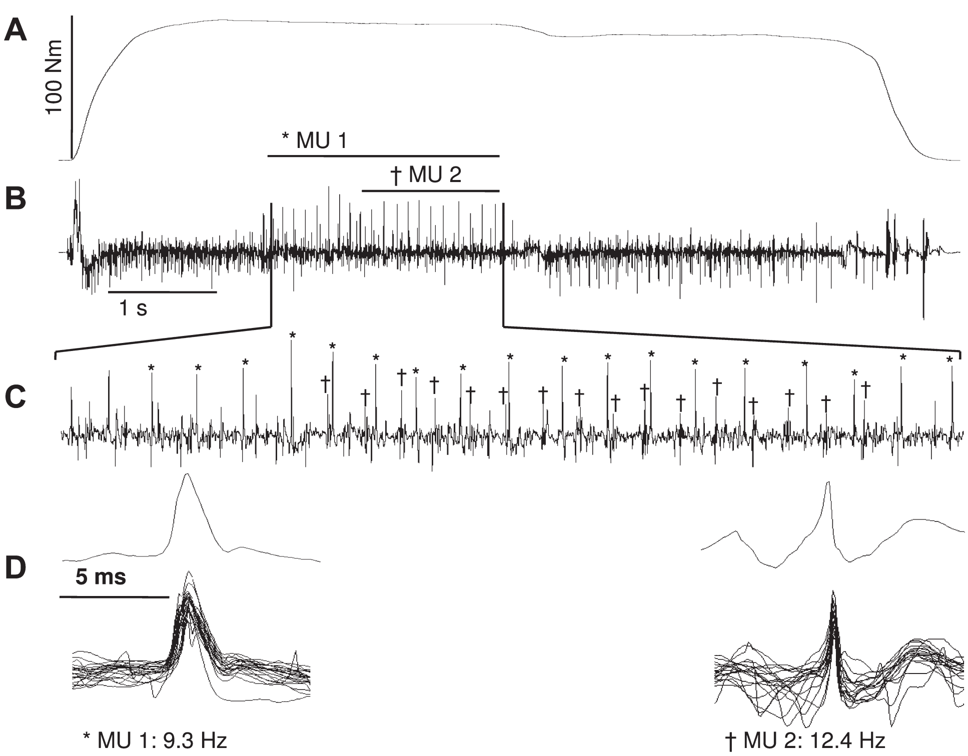

Fig. 1. Examples of typical motor unit (MU) trains of action potentials recorded from the soleus during a maximal voluntary isometric contraction (MVC) of the plantar flexors. *A*: ~6-s torque tracing of a typical MVC performed by an old participant. *B*: EMG recording from 1 of 2 microelectrodes in the soleus. As the intramuscular microelectrode was advanced through the muscle during the MVC, amplitudes of the action potential recordings varied in height in relation to the distance from the recording surface. *C*: a 2-s expanded view of the microelectrode EMG recording, highlighting distinct MU action potential trains. *D*: shapes of distinct action potential shapes used to depict MU trains from the raw EMG signal with an example of overlaid MU action potentials from 2 separate trains below. Firing rates of the MU action potential trains are also provided.

Table 1. *Neuromuscular properties of the plantar flexors*

Neuromuscular Property	Young Men	Old Men
Maximal voluntary isometric contraction, N·m	146.9 (47.2)	96.2 (16.8)*
Voluntary activation, %	99.2 (0.7)	99.0 (0.7)
Evoked peak twitch torque, N·m	12.6 (3.8)	8.6 (3.3)†
Time to peak twitch, ms	122.6 (13.1)	153.2 (10.8)*
Half-relaxation time, ms	94.8 (12.9)	108.2 (13.3)
Contraction duration, ms	217.3 (14.2)	261.5 (18.8)*

Values are means (SD). Neuromuscular properties of the plantar flexors. Old men had significantly weaker maximal voluntary isometric contraction torque, and slower time to peak twitch and contraction duration than the young (*$P < 0.05$). The old men tended to have lower peak twitch torque compared with the young (†$P = 0.08$). Contraction duration is the combination of time to peak twitch and half-relaxation time.

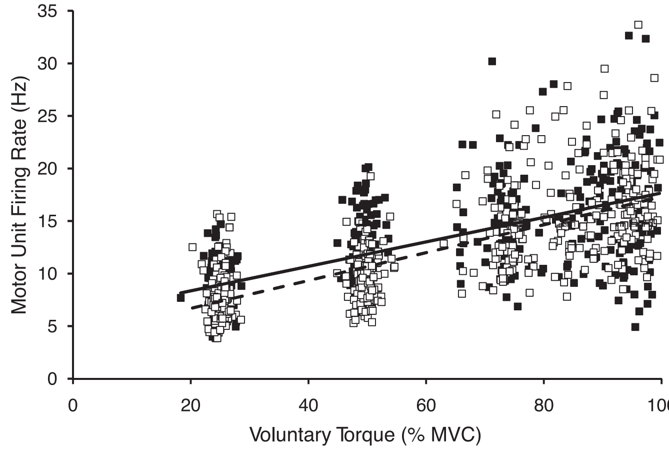

Fig. 2. Scatterplot of normalized voluntary torque level vs. MUFRs for 1,115 [537 and 578 data points for the old (□) and young (■) men, respectively] MU action potential trains. Linear regression equations for the raw data are as follows: $\text{frequency}_{(\text{Hz})}$ (old) = 0.13 × $\text{torque}_{(\%\text{MVC})}$ + 4.04, $r^2 = 0.51$ (dashed line) ($P < 0.05$); and $\text{frequency}_{(\text{Hz})}$ (young) = 0.12 × $\text{torque}_{(\%\text{MVC})}$ + 6.02, $r^2 = 0.42$ (solid line) ($P < 0.05$).

maximal intensities there was a group and contraction intensity effect ($P < 0.01$) for the medial gastrocnemius. RMS amplitude of the medial gastrocnemius normalized to the RMS of the medial gastrocnemius M-wave progressively increased ($P < 0.01$) in both age groups. The old men exhibited higher ($P < 0.01$) RMS amplitudes at 25% and 50% MVC compared with young men for the medial gastrocnemius (Table 2). For the soleus, there was a contraction intensity effect ($P < 0.01$). The normalized RMS amplitude of the soleus progressively increased ($P < 0.01$) in both age groups similarly (Table 2).

A total of 1,115 MU trains was identified based on the criteria outlined in MATERIALS AND METHODS (537 MU trains from the old men and 578 MU trains from the young men). The discrete MU trains identified were similar in number for both groups at all contraction intensities. The total numbers were ~176 MUs at 25% MVC, ~154 MUs at 50% MVC, ~88 MUs at 75% MVC, and ~141 at 100% MVC. Figure 2 depicts a scatterplot of all MUFR (Hz) trains of the soleus in relation to isometric torque output (% MVC). The mean duration for each MU train was ~1.5 s and ~1.3 s with ~16 and ~15 action potentials discriminated per train for the old and young men, respectively. To compare the relationship between MUFRs and normalized torque production, the data set for each age group was fit by linear regression. Similar relationships existed ($P < 0.05$) between the old and young, indicating that MUFRs increased similarly in both groups from low to high contraction intensities (Fig. 2). Individual regression equations for mean MUFRs and absolute voluntary torque were calculated for each subject, and the mean slopes ($P = 0.52$) and intercepts ($P = 0.12$) were not different between groups [0.13 (SD 0.03) and 4.40 (SD 1.67) for the old and 0.12 (SD 0.04) and 6.00 (SD 1.56) for the young, respectively].

When MU trains were binned by contraction intensity, there was a main effect for age ($P < 0.01$) and contraction intensity ($P < 0.01$) and an interaction for age and contraction intensity ($P < 0.05$). Motor unit firing rates increased progressively from 25% MVC to 100% MVC ($P < 0.01$) similarly for both age groups. At contraction intensities of 25% and 50% MVC the rates for the old group were 10% and 20% lower ($P < 0.01$), respectively than the young, but there were no differences in mean rates at 75% ($P = 0.27$) or 100% MVC ($P = 0.86$) (~14.5 Hz and ~16.5 Hz, respectively) (Fig. 3). Furthermore, the range of MUFRs (as indicated by the SDs) was similar between the old and young men at each torque level, which suggests that an equivalent sampling of the motoneuron pool was accomplished for both groups. The overall distribu-

Table 2. *Surface EMG properties of the plantar flexors*

Neuromuscular Property	Young Men	Old Men
MG RMS 25 (% M-wave RMS)	2.4 (0.6)	8.7 (5.2)*
MG RMS 50 (% M-wave RMS)	5.8 (1.8)†	16.3 (8.2)*†
MG RMS 75 (% M-wave RMS)	12.6 (4.9)†	25.5 (11.0)†
Soleus RMS 25 (% M-wave RMS)	2.9 (0.3)	3.1 (0.9)
Soleus RMS 50 (% M-wave RMS)	6.7 (1.3)†	5.8 (1.4)†
Soleus RMS 75 (% M-wave RMS)	10.6 (2.8)†	9.0 (2.0)†
M-wave peak-to-peak amplitude, mV	10.5 (2.5)	5.3 (1.8)*

Values are means (SD). Surface electromyography (EMG) properties of the plantar flexors. Both age groups had higher root mean square (RMS) values at 50% and 75% maximal voluntary isometric contraction (MVC) compared with 25% MVC for both the medial gastrocnemius (MG) and soleus (†$P < 0.05$). Old men had lower RMS at 25% and 50% MVC for the MG, and a lower M-wave peak-to-peak amplitude (*$P < 0.05$) compared with the young.

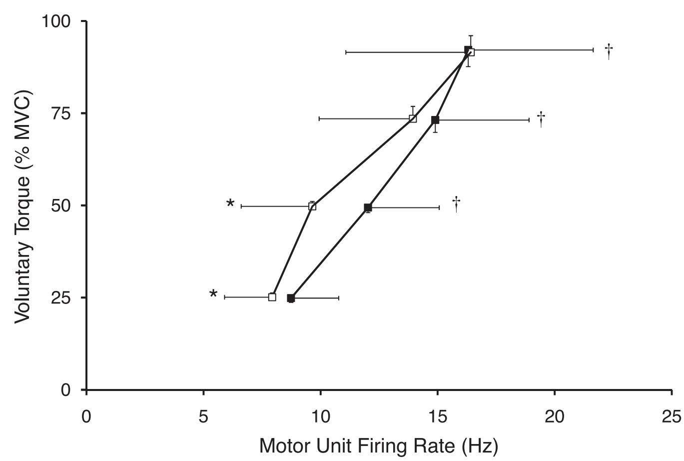

Fig. 3. Mean MUFRs of the soleus over various plantar flexion contraction intensities in old (□) and young (■) men. Axes are reversed from Fig. 2 to be consistent with typical method of plotting stimulated torque-frequency curves. Values are means (SD). Old men had significantly lower MUFRs at 25% and 50% MVC than young (*$P < 0.01$). The MUFRs progressively increased similarly with contraction intensity in both age groups (†$P < 0.01$).

tion of MUFRs grouped for all contraction intensities was similar between the old and young men (Fig. 4). Finally, there was no significant relationship ($P = 0.11$–$P = 0.96$) between MUFRs and contractile speed parameters (TPT, HRT, and CD) for any contraction intensity (Fig. 5).

DISCUSSION

Despite a mean difference in age of ~52 yr in combination with lower strength and slower contractile speeds in the old men compared with the young, MUFRs were not different at the higher contraction intensities (75% MVC and 100% MVC), but were less in the old at the lower contraction intensities (25% and 50% MVC). These results are at odds with most previous studies in other muscles in which rates are reduced in healthy aged subjects, particularly at contraction intensities at or greater than 50% MVC (4, 20, 21). Furthermore, no significant relationship was found between MUFRs of the soleus and the contractile speed of the triceps surae. Thus it appears at least for this muscle group that an association between MUFRs and muscle contractile properties is not obligatory when the system is altered by aging, even in healthy subjects. Despite some inherent limitations in this and other models centering on this topic, the current findings support our hypothesis and highlight one important concept: that age-related adaptations may be muscle specific.

Strength, voluntary activation, and contractile properties. Our results confirm that triceps surae voluntary isometric strength is 35% less and contractile speed measures are ~20% slower in old compared with young men (30, 49, 58). These are similar to reports for other lower limb muscles (40). Peak twitch torque also tended to be lower in the old men compared with the young ($P = 0.08$), which is similar to previous studies in this muscle group (49, 58). There was no difference between old and young men for voluntary activation in that both age groups were capable of near-maximal activation (~99%), and thus weakness is likely related to structural and functional changes within the muscle (14, 34, 52, 60). Some studies (7, 30), but not all (49, 58), have reported lower voluntary activation for the plantar flexors of old adults compared with the young. This discrepancy may be related to this specific muscle group (25), the technique (25), or to practice (15, 17) and the

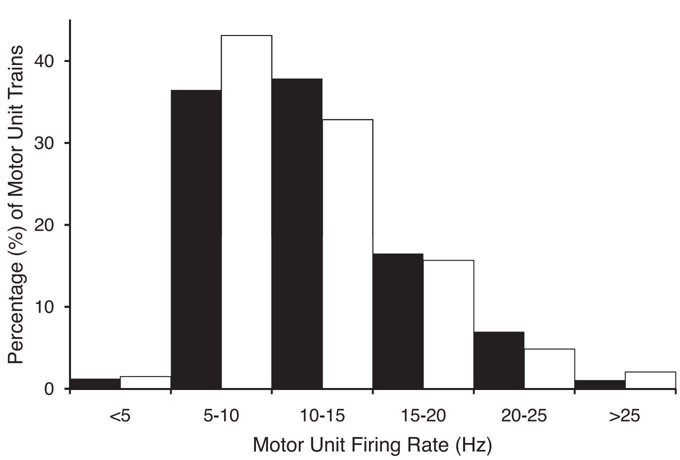

Fig. 4. Histogram represents the distribution of pooled MUFRs of the soleus across all plantar flexion contraction intensities for old (open bars) and young (filled bars) men (bin width 5 Hz). No difference between old and young men.

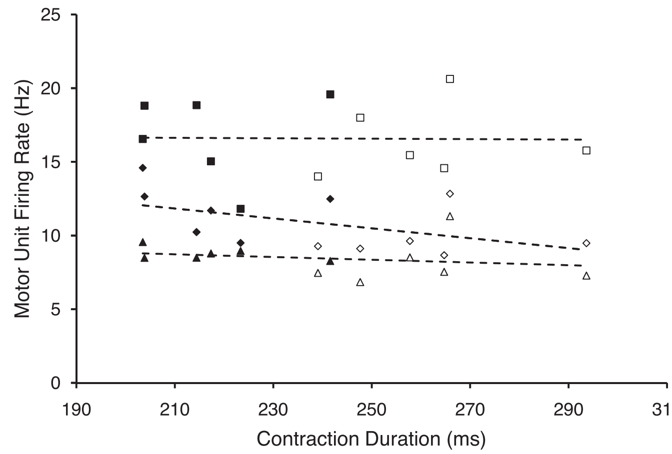

Fig. 5. Relationship for individual mean twitch contraction durations and individual mean MUFRs collected at 25% (triangles), 50% (diamonds), and 100% (squares) MVC for old (open symbols) and young (filled symbols) men. Pearson correlation coefficient (r) at 25%, 50%, and 100% MVC were $r = -0.22$, -0.49, and -0.02, respectively. The R^2 values at 25%, 50%, and 100% MVC were $R^2 = 0.05$, 0.24, and <0.01, respectively. No relationship existed at either contraction intensity ($P = 0.11$–$P = 0.96$).

quality of the subjects. For example, reports on the elbow flexors and extensors suggest that if ample practice is provided that old men can achieve similar activation levels as young men (15, 17). In the present study our subjects were healthy active subjects who were well practiced with this procedure.

Motor unit properties. Our results provide a comprehensive evaluation of the relationship between contractile intensity and MUFRs, and whether this relationship is altered with aging. The present results support the contention that the soleus exhibits uniquely low maximal firing rates in both old and young men. In the young men we found a mean MUFR of 16.5 Hz at 100% MVC which is ~20 to 70% lower compared with most other limb muscles (For review, see Ref. 11), except for the extensor hallucis longus with a maximum mean rate of almost 17 Hz (29). To date, only one other study has reported mean maximal MUFRs in the soleus, and they reported a mean firing rate of ~11 Hz in three subjects aged 30–55 yr (3). This is lower than that of the present study, but the dissimilarity may be attributed to the small sample size in the earlier study (3) and methodological and MU analysis differences. Nevertheless, the fundamental outcome of very low maximal firing rates for the soleus is in agreement.

These low rates, regardless of age, may be a result of the motor control strategy and functional requirements (33, 59) as well as the morphological composition of the soleus (~80–90% slow twitch) (18, 57). The low MUFRs in this active postural muscle (33) across a range of contraction intensities including maximum (Figs. 2 and 3) suggests that there is a greater reliance on MU recruitment rather than rate coding for torque gradation, which may be especially important during plantar flexion with a flexed knee. Indeed, these results are in support of a recent report that suggests MUs in the soleus are recruited up to contraction intensities close to maximum (36). Although some investigators report that lower threshold MUs discharge at higher rates than subsequently recruited MUs as target torque increases (9, 12), this is not always found (36, 59), especially in postural muscles. For example, in the soleus early recruited MUs did not display the highest MU discharge rates, and there was no correlation between recruitment threshold and MUFRs from low intensity to maximum (36). Finally, because of the slow contractile properties of the soleus tetanic fusion may be achieved with low rates of excitation as suggested by Bellemare et al. (3).

With aging these already low MUFRs were not further reduced at high intensities (75% MVC and 100% MVC). This result is at variance with findings from most other muscle groups tested. Postural function and thus chronic activity of the soleus (33) in ambulatory subjects may help to minimize any reduction in the discharge rates of the MU pool in these healthy old men, or this muscle may represent a lower limit to the range of rate coding that is useful for effective force control. Although there is an age-related diminution of muscle mass in the soleus as perhaps represented by the smaller M-wave amplitude, which is typical in this (58) and other muscles (31), the soleus muscle volume and physiological cross-sectional area seem to be much better preserved than the medial and lateral heads of the gastrocnemius (34). Furthermore, unlike other muscles tested to date, we reported a minimal reduction in the number of functional MUs (7) well into the eighth decade of life for the soleus. In relation to these data, Kanda et al. (22) concluded that long-term physical activity may retard MU declines in alpha-motoneuron soma size and number of alpha-motoneurons that might be a result of normal aging, and in the rat soleus the number of motoneurons are unchanged with age (16). Hence, the old and young men in this study may have MU pools of a comparable size and distribution and thus produce a similar modulation of firing rates contributing to the gradation of torque. This is expressed by the similarity of the linear relationships between contraction intensity and MUFR found for both the old and young men (Fig. 2). The relatively small range of rate coding (<10 Hz) in the soleus from ~7–8 Hz to ~17 Hz (25% to 100% MVC) compared with other muscles irrespective of aging (4, 47) may represent a physiological limitation for effective motor control. Thus, for a healthy active subject, soleus firing rates at high intensities cannot be significantly reduced with aging if normal function is to be maintained. These results in combination with previous studies that reported minimal deteriorations of gross muscle size and MU numbers that could affect torque output (7, 34) lead us to conclude that age-related remodeling (31) may be blunted or much delayed in the postural soleus muscle composed of more than 80% type I MUs (18, 56).

Previous studies in other limb muscles suggest that greater age-related differences in MUFRs exist at higher rather than lower contraction intensities (≥50% MVC) (20, 21). We observed the opposite with lower MUFRs for the old men found only at 25% and 50% MVC, which agrees with a recent report from our group at 20% and 30% MVC in the soleus using a different indwelling needle sampling technique (7). Additionally, our MUFR data at 25% (~8 Hz) and 50% MVC (~12 Hz) in the young men are similar to previous reports (6, 27, 32) that used different techniques to record from threshold (~7 Hz) to ~60% MVC (~11 Hz). The reduced firing rates at low (25% MVC) to moderate (50% MVC) torque levels for the old compared with young men may be related to the age-related slowing in contractile speed in the soleus (58). This slowing presumably should shift the stimulated torque frequency curve to the left, as demonstrated previously for this and other muscle groups (8, 41), allowing a given relative torque to be achieved with lower MUFRs especially during the steep portion of the curve. However, we did not find any relationship between the age-related slowing in contractile speed of the triceps surae and mean MUFRs in the soleus (Fig. 5). This may represent a limitation of this muscle model per se, or the relationship between the gastrocnemius and soleus for torque gradation may be modified with aging, particularly at submaximal contraction intensities.

Generally it is reported that MUFRs (≥50% MVC) are lower and whole muscle contractile properties slower in old men compared with young (40). Motor unit firing rates may be reduced in the old compared with young subjects due to age-related alterations anatomically and physiologically at the cortical level (10, 35, 39, 43, 50) and morphological changes in the neuromuscular system, such as a loss of motoneurons (31) or demyelination of remaining motoneurons (57), as well as changes in motoneuron excitability (24), whereas whole muscle contractile property speed is related to mechanisms within the muscle, such as fiber type composition (60), calcium handling (14) and architecture (52). The above processes may change coincidentally in parallel or there may be a coordinated relationship that is retained for optimal torque gradation as the system undergoes aging. Based on correlative data, previous studies have suggested that contractile function is actively coordinated with neural output as the system ages (4, 41), but the present results suggest that maintenance of this relationship is not obligatory with aging or is modifiable.

RMS amplitudes were higher for the old men compared with the young at submaximal intensities (25% and 50% MVC) for the medial gastrocnemius. In combination with reduced MUFRs in the soleus, our data suggest that motor control strategies for the triceps surae are altered with aging during low to moderate contraction intensities. It has been shown that old adults have reduced motor control capabilities for effective muscle coordination. This includes an inability to target quickly (2), difficulty coactivating multiple muscles or muscle groups during a multi-joint task (46), greater ratio of coactivation during different isometric tasks (26, 51), and greater force fluctuations (55) than the young. Shinohara et al. (48) suggested that if torque-generating capabilities of synergistic muscles change disproportionately, then previously established motor control strategies to these muscles are possibly suboptimal. If these neural commands are permanently altered (i.e., aging), these muscle synergies and motor control strategies need to be modified (48). Thus the accentuated age-related degeneration of the gastrocnemius compared with the soleus (34) may alter the previously suitable neural commands for smooth torque generation in this particular muscle group. Furthermore, due to these disproportionate architectural changes with age in the triceps surae (34), flexing the knee angle to 90° may not limit the gastrocnemius torque contribution to plantar flexion in the old men to the same extent as reported in the young (5). Because the normalized soleus EMG is similar between our old and young men and MUFRs are less in the old men than the young at 25% and 50% MVC, greater recruitment may occur in the soleus of the old during these low to moderate contraction intensities.

Summary. The human soleus, like the vastus medialis, does not demonstrate the often-reported reduction in high-intensity MUFRs reported for other muscle groups in healthy aged humans. This is despite the age-related contractile slowing found for the whole triceps surae, of which the soleus makes a substantial (>70%) contribution. Similar studies have suggested that an appropriate relationship between whole muscle contractile speed and firing rates of constitutive units is maintained with aging, but the present results indicate that this is a mutable relationship that may depend on the function of the muscle rather than aging per se. These results support the contention that not all skeletal muscles are affected equally by the aging process, and generalizations cannot be stated. Clearly, further studies are indicated to understand the relationship between function (habitual activity) and aging.

GRANTS

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DISCLOSURES

No conflicts of interest are declared by the authors.

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