ABSTRACT: The documented impact of contractile level on decomposition-enhanced spike-triggered averaging motor unit number estimates (MUNEs) in young adults demonstrates the importance of selecting an objective contraction intensity that yields the most representative MUNE for a given muscle. Whether the same contraction intensity would be ideal in an altered system (e.g., by aging or disease) has yet to be examined. Thus, the main purpose of this study was to compare the effects of contraction intensity on MUNEs from the soleus muscle in young (≈27 years) and old (≈75 years) men. Using decomposition-enhanced spike-triggered averaging, surface and intramuscular electromyographic signals were collected from the soleus during a range of submaximal isometric plantar-flexion contractions (threshold, 10%, 20%, and 30% of maximum voluntary contraction; MVC). Five MUNEs were calculated, one for each of the four contraction intensities and an ensemble MUNE was derived from all MUs collected. Although MUNE decreased similarly with increased effort in both groups, MUNEs were not significantly reduced in the old men compared to the young men. Consequently, the ensemble MUNE was extrapolated to an intensity of ≈15% MVC in both young and old. The results suggest that, in the soleus, the use of the same contraction intensity across age groups is a valid comparison.

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AGE-RELATED REDUCTIONS IN THE ESTIMATED NUMBERS OF MOTOR UNITS ARE MINIMAL IN THE HUMAN SOLEUS

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The aging process is associated with a loss of skeletal muscle mass and a concomitant decrease in muscle strength.[15] Although the factors contributing to these age-related declines are not completely understood, some may be related to a reduction in the number of functioning motor units (MUs) and the inability of the surviving motor axons to reinnervate viable muscle fibers that remain after the loss of an axon. A variety of studies suggest that losses of MUs and muscle strength occur gradually during the initial seven decades of life, but that the declines are accelerated in the following decades.[9,10,12,30,38]

Age-related decreases in motor unit number estimates (MUNEs) have been reported in a variety of upper-limb muscle groups,[10,11,16,19,22,42] although one study has demonstrated preservation in the number of functional MUs in the biceps brachii.[22] In the lower limb the extensor digitorum brevis reportedly has fewer MUNEs with old age,[12,22,36] but the susceptibility of the deep peroneal nerve to trauma, even in healthy young adults,[24] makes this muscle a poor model of biological aging. Only two studies have explored MUNE and aging in more proximal and functional lower-limb muscles.[30,46] Recently, McNeil et al.[30] demonstrated a 40% reduction in MUs of the tibialis anterior (TA) between the 3rd and 7th decades and a further 33% reduction between the 7th and 9th decades. Vandervoort and McComas[46]

Abbreviations: ANOVA, analysis of variance; DE-STA, decomposition-enhanced spike-triggered averaging; EMG, electromyography; MU, motor unit; MUNE, motor unit number estimate; MUP, motor unit potential; MVC, maximum isometric voluntary contraction; RMS, root mean square; S-MUP, surface motor unit action potential; SOL, soleus; TA, tibialis anterior

Key words: aging; electromyography; isometric strength; motor unit number estimation; rate-coding

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reported a 70% lower MUNE in the soleus (SOL) of very old adults (≈90 years) compared to young to middle-aged adults (5–50 years; no mean reported) from a different study.[28] Thus, it seems that the number of functional MUs declines with age, but the magnitude of loss depends on the age of the elderly participants and may vary from muscle to muscle.

Many methods exist to derive a MUNE.[8] One method, decomposition-enhanced spike-triggered averaging (DE-STA), previously described in detail,[45] is a reliable and valid technique.[6,7] However, it has been demonstrated in young subjects that sampling of MUs has a significant impact on the sample of MUs collected[5,14,29] and, consequently, the MUNE. High-intensity contractions may preferentially sample large MUs and result in a smaller MUNE, whereas smaller MUs and a larger MUNE correspond to lower-intensity contractions. It is reasonable to assume that the most representative MUNE would be obtained at the contraction intensity that encompasses small and large MUs in proportions appropriate to the given muscle.[29] Aging is associated with denervation and collateral reinnervation of muscle fibers, a process that leads to remodeling of MUs.[23] The presence of larger, more homogenous MUs in the muscles of older individuals may alter the contraction intensity effect on MUNEs, but this has not been investigated. Furthermore, the contraction intensity at which the most representative MUNE is obtained could also be affected, and this would impact the validity of comparing MUNEs across age groups at the same intensity.

Thus, the purposes of the present study were: (1) to determine the effect of contraction intensity on MUNEs in an aged muscle, and (2) to compare MUNEs in the SOL of young and old men using DE-STA. We hypothesized that aging would reduce the contraction intensity effect on MUNEs in the old men due to extensive age-related MU remodeling. This remodeling process would shift the most representative sample toward a larger contraction intensity. Second, we hypothesized the old men would have fewer MUs than young men in the SOL due to the documented decreases in MU numbers with aging in this and other muscles.

MATERIALS AND METHODS

Subjects. Nine young men (27 ± 3 years) were recruited from the university population, and nine old men (75 ± 2 years) were recruited from a university-based recreation program. This program is designed to maintain cardiovascular fitness, flexibility, and muscular endurance. Thus, all participants were considered healthy, recreationally active for their respective age group, and free of neuromuscular disease. All older subjects had normal reflexes, strength, and sensation in the lower limbs, with no clinical features of focal or generalized neuropathy. The local ethics review board approved the study. All participants gave informed written and oral consent. There were no differences in the mean height and weight of the young and old groups (174 ± 8 cm and 82 ± 11 kg, and 176 ± 6 cm and 86 ± 13 kg, respectively).

Experimental Arrangement. A Biodex System 3 dynamometer (Biodex Medical Systems, Shirley, New York) was used to record plantar-flexion torque in the isometric mode. Subjects were seated comfortably in a reclined position with the hip angle at ≈90°, knee at ≈90°, and ankle at ≈90° (neutral). Testing was conducted on the dominant (right) leg. Velcro straps secured the foot across the toes and dorsum. The subjects were securely fastened with straps around the shoulders, waist, and thigh to prevent extraneous movement during isometric plantar flexion.

Ag–AgCl resting electrocardiogram electrodes (1 × 1.5 cm; Marquette Medical Systems, Jupiter, Florida) recorded the surface electromyographic (EMG) signals. The EMG recording sites were cleaned with alcohol prior to electrode placement. The active electrode was positioned over the lateral aspect of the SOL to minimize the rise time and maximize the negative-peak amplitude of the maximum M-wave. The reference electrode was placed on the Achilles tendon at the level of the malleoli, and a ground electrode was positioned over the patella. Intramuscular EMG signals were recorded by a disposable concentric needle electrode with a recording surface of 0.03 mm^2 (Model N53153; Teca, Hawthorne, New York) inserted into the lateral aspect of the SOL, 5–10 mm away from the active surface electrode.

Experimental Procedures. EMG data were acquired utilizing DE-STA software on the Neuroscan Comperio system (Neurosoft, El Paso, Texas). DE-STA and its associated algorithms have been previously described.[17,44,45] Intramuscular EMG signals were bandpass filtered from 10 Hz to 10 kHz. The surface EMG signals were filtered at 5 Hz to 5 kHz. The maximum M-wave was evoked via supramaximal stimulation of the tibial nerve at the popliteal fossa using a Digitimer™ stimulator (Model DS7A; Digitimer, Welwyn Garden City, UK). Current intensity was progressively increased until a plateau in the

M-wave amplitude was achieved. At this point the current was increased 15% to ensure that all motor axons were activated. During the determination of the M-wave the active electrode was repositioned to maximize the negative-peak amplitude and minimize negative-peak rise time. Subsequently, to determine maximal torque during plantar-flexion, three maximum isometric voluntary contractions (MVC) were performed with 3-min rest periods between contractions. The peak torque of the three attempts was taken as the subject's MVC. Each MVC lasted ≈5 s, and visual torque feedback was provided via a computer monitor. In addition, investigators provided each participant with strong verbal encouragement during the MVC trials.

During the first MVC the peak root mean square (MVC-RMS) value of the surface EMG signal was calculated over a 1-s interval. To determine central activation the interpolated twitch technique was used. During the second MVC attempt a supramaximal doublet (D_s) was delivered with an interpulse interval of 10 ms. This doublet was compared to a doublet (D_r) that was evoked at rest following the second MVC in an attempt to quantify central activation {% activation = [1-(Ds/Dr)] × 100}. If the subject's MVC revealed an interpolated twitch, the central activation protocol was delivered again during the third MVC attempt.

Upon completion of the MVCs subjects were given a 5-min rest before commencement of contractions with simultaneous surface and intramuscular EMG recordings. Motor unit potential (MUP) trains were collected at four different contraction intensities (threshold, 10%, 20%, and 30% MVC) and their order was randomly assigned. Threshold was considered the initial presence of the first two or three MUs recruited by the SOL during a minimal plantar-flexion contraction. For contractions at 10%, 20%, and 30% MVC subjects were instructed to match their torque output with target lines on the computer monitor.

With the concentric needle inserted the subject was instructed to contract the SOL minimally while the operator manipulated the electrode to minimize rise times of the negative-peak amplitudes of the first two or three detected MUPs. Once the operator was satisfied with the electrode position, the subject was instructed to increase torque up to the appropriate target level within 1 to 2 s. At this point the operator initiated the intramuscular and surface EMG recordings, which lasted 30 s, while the subject produced continuous, stable isometric plantar-flexion torque. One minute of rest was given between contractions. After each contraction the needle was repositioned either to a different depth or reinserted into a different part of the muscle belly. Upon the collection of 20 or more MUs at a given contraction intensity the same procedures were repeated for all subsequent contraction intensity levels. We needed 4–11 contractions for a sufficient collection of MUs at each contraction intensity.

Data Reduction and Statistics. During off-line analysis, decomposed EMG signals were reexamined to determine the acceptability of the needle-detected MUP trains and the corresponding surface motor unit action potentials (S-MUPs). The selection criteria followed a specific order. First, an acceptable MUP train required greater than 50 detected discharges, which were used as triggers for spike-triggered averaging. Second, the MU firing pattern was inspected visually for a consistent firing rate (i.e., a coefficient of variation ≤30) and a physiological mean firing rate. Finally, the interdischarge interval histogram was examined to confirm that it was a Gaussian distribution. If a MUP train did not fit any one of these criteria it was excluded from further analysis.[6]

S-MUPs were inspected to determine whether a distinct waveform was present and that it was temporally linked to the needle potential. Further, the computer-generated negative-peak onset and negative-peak amplitude markers of the acceptable S-MUPs were inspected to ensure that they were accurate. If not, they were manually reset. Next, a computer algorithm aligned the negative-peak onset markers and created a mean S-MUP template based on a data-point by data-point average.[18] An MUNE was then derived by dividing the negative-peak amplitude of the M-wave by the negative-peak amplitude of the mean S-MUP. Additionally, in an attempt to provide the most representative data, ensemble values for MUNE, S-MUP negative-peak amplitude, and MU firing rate were calculated by pooling all MUs collected, regardless of contraction intensity. The ensemble MUNE value was then used to extrapolate a relative contraction intensity that would yield, in theory, the same result without the need for data collection at multiple intensities,[29] thereby saving considerable data collection time for clinicians and researchers alike.

Torque data were sampled at 100 Hz using a 12-bit A/D converter (model Power 1401; Cambridge Electronic Design, Cambridge, UK) and sampled online using Spike2 software (Cambridge Electronic Design). Offline analysis with Spike2 was used to determine voluntary and evoked isometric

Table 1. Neuromuscular properties of the plantar flexors.

Group	MVC (Nm)	Pt (Nm)	TPT (ms)	HRT (ms)	NegPk-Amp (mV)
Young (n = 9)	170.7 ± 35.3	17.3 ± 3.2	127.1 ± 15.2	105.8 ± 14.3	22.4 ± 2.2
Old (n = 9)	122.5 ± 30.9*	19.9 ± 5.2	160.4 ± 17.0*	126.2 ± 19.2*	16.3 ± 4.0*

Absolute isometric maximal voluntary contraction (MVC) torque, evoked twitch torque (Pt), time-to-peak twitch torque (TPT), half relaxation time (HRT), and negative peak amplitude of the soleus M-wave (NegPk-Amp). Values are means ± standard deviation. Old men had significantly weaker MVC torque, slower TPT and HRT, and lower NegPk-AMP than the young men ($P < 0.05$).*

torques as well as time-to-peak torque and half-relaxation time of the twitch.

All data were analyzed using SPSS v. 15 (Chicago, Illinois). Subject and twitch characteristics as well as torque data were analyzed using a univariate analysis of variance (ANOVA). A Mann–Whitney *U*-test was performed to analyze central activation between groups. A two-way ANOVA with repeated measures was used to analyze all other data. F ratios were considered significant at $P<0.05$. If significant main effects or interactions were present, a Tukey's post-hoc procedure was conducted to determine where the differences existed. Descriptive statistics include means ± standard deviation for both the text and figures.

RESULTS

Strength, Central Activation, and Twitch Characteristics. Despite similarities in height and weight, the old men produced 39% less maximal isometric plantar-flexion torque than the young men (Table 1). Central drive, as assessed by the interpolated twitch technique, was significantly lower in the old than young men (88% and 99%, respectively). Unlike voluntary strength, peak twitch torque was similar in both groups (Table 1). In contrast, time-to-peak torque and half-relaxation times were significantly slower in the old than young men (26% and 19%, respectively). Both groups were equally capable of tracking the various target torque levels (10%, 20%, and 30% MVC) with little error. At threshold, however, torque was significantly higher for the old than young (Table 2).

Motor Unit Properties. The number of MUP trains sampled was 802 (≈89 per subject) and 932 (≈102 per subject) from the old and young men, respectively. The RMS value of the raw surface EMG signal during the targeting contractions expressed as a percentage of the MVC-RMS was significantly greater at all contraction intensities in the old men than the young (Table 2). There was no difference in mean MU firing rate for the old men with increasing contraction intensity from threshold to 30% (7.3 ± 0.3 and 7.9 ± 0.7, respectively), but the mean MU firing rate increased in the young men (7.9 ± 0.2 to 9.9 ± 1.0 Hz at threshold and 30%, respectively) (Table 2). Additionally, mean MU firing rate was lower (12% and 24%) for the old than young men at 20% and 30% MVC, respectively (Table 2). The ensemble firing rate was 14% lower in the old men than the young (Table 2).

The negative-peak amplitude of the maximum M-wave was significantly smaller (38%) in the old men than the young (Table 1). The mean S-MUP negative-peak amplitude was significantly smaller (32%) for the old men at 30% MVC than the young. There were no group differences in mean S-MUP negative-peak amplitude at any other contraction intensity (Table 2). The mean S-MUP negative-peak amplitude increased significantly for both groups with an increase in contraction intensity (Table 2). The overall change from threshold to 30% MVC was 87% and 167% in the old and young, respectively. For both groups the ensemble mean S-MUP negative-peak amplitude was a value between the 10% and 20% MVC mean S-MUP negative-peak amplitudes (Table 2).

Unlike mean S-MUP data, the mean MUP peak-to-peak amplitude did not differ with an increase in contraction intensity in either age group (Table 2). However, old men had mean MUP peak-to-peak amplitudes that were greater than those of the young by 55%–86% across the range of intensities. Duration of the mean MUP decreased with increasing contraction intensity in the old, but was similar across all intensities in the young (Table 2). For all contraction intensities other than 30% MVC, mean MUP durations were 19%–26% longer for the old men compared to young (Table 2). At threshold, one old subject was incapable of recruiting a sufficient number of MUP trains to collect a time-efficient MUNE.

Because of an increase in mean S-MUP negative-peak amplitude, MUNEs for both age groups decreased with increasing contraction intensity. There were no age-related differences in MUNEs for the

Table 2. Electrophysiological properties of the soleus with increasing contraction intensity.

Contraction intensity	Mean MUFR (Hz)		Mean S-MUP NegPk-Amp (μV)		MUP P-P Amp (μV)		MUP Dur (ms)		Target RMS (% MVC-RMS)		Target torque (% MVC)	
	Young	Old	Young	Old	Young	Old	Young	Old	Young	Old	Young	Old
Threshold	7.9 ± 0.2	7.3 ± 0.3	25.2 ± 14.0	27.7 ± 10.9	580.4 ± 88.7	929.7 ± 263.4*	10.3 ± 1.1	13.0 ± 1.3*	4.2 ± 1.1	9.4 ± 1.8*	4.8 ± 0.9	6.5 ± 1.0*
10%	8.3 ± 0.4	7.6 ± 0.6	34.4 ± 14.4	34.1 ± 12.3	607.5 ± 102.4	1132.8 ± 426.9*	9.9 ± 1.2	12.0 ± 0.5*	6.4 ± 1.9	11.5 ± 2.3*	10.0 ± 0.2	10.6 ± 0.7
Ensemble	8.8 ± 0.5†	7.7 ± 0.5*	42.3 ± 14.4†	37.2 ± 8.5	642.3 ± 58.3	1078.9 ± 264.7*	9.9 ± 0.9	12.0 ± 0.8*	9.9 ± 2.6	13.5 ± 2.1*		
20%	8.8 ± 0.6†	7.7 ± 0.9*	44.7 ± 10.5†	41.6 ± 10.6	636.1 ± 69.5	1077.0 ± 271.0*	9.9 ± 0.8	11.8 ± 1.4*†	11.0 ± 2.0	16.4 ± 3.5*	20.0 ± 0.4	20.1 ± 0.6
30%	9.9 ± 1.0§	7.9 ± 0.7*	67.2 ± 21.0§	50.8 ± 6.8*‡	723.0 ± 107.6	1122.0 ± 302.6*	10.0 ± 0.8	11.3 ± 1.4†	17.1 ± 4.4	22.4 ± 4.4*	30.1 ± 0.4	29.8 ± 0.6

Contraction intensities are expressed subjectively or as a percentage of the maximum voluntary contraction (MVC) torque. Threshold refers to the torque level at which the first 2 or 3 MUs are recruited, whereas ensemble refers to the extrapolated torque level (~15% MVC) obtained by pooling the data from the other four torque levels. Mean motor unit firing rate (MUFR), mean surface motor unit action potential negative peak amplitude (S-MUP NegPk-Amp), mean motor unit action potential peak-to-peak amplitude (MUP P-PAmp), mean motor unit action potential duration (MUP Dur), surface EMG recorded during the 30-s targeting contraction (expressed as a percentage of the peak root-mean square achieved over a 1-s interval during the MVC; MVC-RMS), and torque recorded during the 30-s targeting contraction (expressed as a percentage of the MVC). Values are means ± standard deviation.

**Significant age effect,*

†significant from threshold,

‡significant from threshold and 10%,

§significant from threshold, 10%, ensemble and 20% ($P < 0.05$).

FIGURE 1. Comparison of MUNE in young (filled bars) and old men (open bars) at varying contraction intensities. Values are means ± standard deviation. No age effect. Ensemble, 20% and 30% MUNEs were significantly smaller than threshold (*$P < 0.05$).

ensemble or at any contraction intensity (Fig. 1). However, there was a trend ($P = 0.08$) toward a lower MUNE for the old compared to young only at the threshold level. The mean MUNEs for the old and young at threshold were 675 ± 336 and 1101 ± 486 MUs and progressively decreased to 323 ± 78 and 356 ± 90 MUs by 30% MVC, respectively (Fig. 1). The ensemble MUNE for the old and young was 458 ± 151 and 578 ± 170 MUs, respectively. These numbers represented a value between 10% and 20% MVC MUNEs for both age groups (Fig. 1). The ensemble estimate was extrapolated to a contraction intensity of ~15% MVC.

DISCUSSION

In contrast to our hypotheses, contraction intensity effects on MUNEs were similar in young and old men and, consequently, the intensity at which the most representative MUNE (15% MVC) was obtained did not change with age. Further, MUNEs were not significantly lower with age at any contraction intensity. These results suggest that with aging the motor axons innervating SOL muscle fibers may be well preserved into the 8th decade of life, despite a loss of strength and slowing of contractile properties and MU discharge rates.

Central Activation, Strength, and Contractile Properties. In the present study, similar to previous findings,[3,33] the young were capable of near-maximal activation (>99%) of the plantar-flexors. In contrast, the old men were only able to activate to 88%, a finding in keeping with recent plantar-flexor studies

on older populations.[20,33,43] Due in part to the submaximal activation in the old, there was a decrease in plantar-flexor maximal voluntary strength with age. These results mirror those of Vandervoort and McComas[46] and are also quite similar to other, more recent studies.[33,34] Other factors may have contributed to the age-related decrease in strength, which include alterations in muscle architecture,[37] decrease in contractile cross-sectional area,[35] increased co-activation,[27] and a decrease in fiber-specific tension.[21] In the current study, contractile properties were slower in the old men, confirming previous reports for this muscle,[43,46] and peak twitch torque was not different, which has often been reported.[13,31]

Motor Unit Properties. Despite a narrow rate-coding range in the SOL from ≈6.6 ± 0.6 Hz at threshold[32] to 10.7 ± 2.9 Hz at maximum effort,[4] the MU discharge rates of our old men were less than those of the young at ensemble, 20% and 30% MVC. This reduction may have occurred in association with an age-related leftward shift in the force frequency curve.[1,2] Connelly et al.[13] demonstrated indirectly that slower contraction durations were matched by slower MU discharge rates in the TA of old men. This matching process between the contractile ability of the muscle and neuromuscular control may be to optimize the efficiency of contractions in aged muscle.[39] Thus, our old men were capable of producing a similar relative torque with a lower MU discharge rate than the young.

Similar to previous reports,[40,46] the maximum M-wave amplitude was reduced in the old men compared to the young in our study. A reduction in M-wave amplitude may be due to a decrease in the number of muscle fibers secondary to age-related MU losses or a reduction in muscle mass secondary to muscle fiber atrophy, or both. The nonsignificant decrease in MUNEs in the present study suggests that the loss of functional MUs is probably not a large contributor to the M-wave amplitude reduction.

In contrast to recent evidence of extensive age-related MU remodeling,[30] the present results demonstrated that the S-MUP negative peak amplitude was not larger in the old men than the young. It was significantly smaller in the old compared to the young men at 30% MVC. It is difficult to determine the potential mechanisms that caused this apparent contradiction. According to the present results, the aging SOL, unlike the TA, may not undergo the substantial collateral reinnervation (MU remodeling) following motor axon loss that is characteristic of aging muscles.[23] Instead, muscle fiber atrophy or loss in higher-threshold MUs within the SOL could account for the smaller S-MUP amplitude at 30% MVC (and the smaller M-wave) in the old men. The age-related increases in the amplitude of the intramuscular EMG data lend credence to the possibility of muscle fiber atrophy. A reduction in muscle fiber size with a preservation of motor axons would increase the density of the number of muscle fibers within the concentric needle recording area and consequently increase the size of the mean MUP amplitude.

In our study the ensemble MUNE in the old men was not significantly reduced compared to the young. This atypical observation has been reported in only one other study to date,[22] but for a different muscle group. In that study it was speculated that collateral reinnervation was limited in the aging biceps brachii and that a decrease in the M-wave amplitude was entirely the result of intrinsic changes in the muscle fibers.[22] It is possible that the motor axons innervating the SOL are well maintained in healthy, active individuals in their 8th decade of life. For example, it has been reported in rats that long-term physical exercise slowed the age-related changes in motoneurons and peripheral nerves.[26] Thus, the frequent activity of the SOL as a postural muscle[25] could maintain motor axons and thus MU health.

Our observation of a nonsignificant decrease in MUNEs with age contradicts the 70% decrease previously reported in the SOL using the incremental stimulation technique.[46] In that study, MUNEs were obtained from a subset of five of the oldest subjects and these values were compared to those collected previously from a young to middle-aged group.[28] The present estimate that we believe to be most representative of the actual number of MUs in the SOL (ensemble = 578 MUs) does not match the value (957 MUs) previously reported in the young to middle-aged population.[28] Instead, the young value estimated by McComas[28] more closely resembles our threshold MUNE (1101 MUs). The reason for the disparity may be that in our study the ensemble MUNE was derived from MUs collected at different contraction intensities and thus MUs of varying sizes. The incremental technique[28] is based on assumptions that may overestimate a MUNE, i.e., it assumes that MUs activated at low stimulus intensities are representative of the whole population and that each response represents a single MU. The former assumption is difficult to test, but the latter assumption is known to be false because of the presence of alternation.[41] Although the use of DE-STA rather than the incremental method may explain the lower

MUNEs of our young, it fails to explain why Vandervoort and McComas[46] reported lower MUNE values in their old group compared to our old men (283 and 458 MUs, respectively). Two reasons for this discrepancy may be the very small sample size in the other study and the lower mean age of our elderly group (75 years) in comparison to the other study (≈90 years). It was recently demonstrated in the TA[30] that the number of MUs decreases at a dramatic rate from the 7th to the 9th decade of life, i.e., there was a 40% reduction from age 27 to 66 years and another 33% decline between the ages of 66 and 82 years. Thus, the difference between the present study and that of Vandervoort and McComas[46] may be due to an accelerated decline in the number of functional MUs that occurs at a slightly older age in the SOL than the TA.

In the present study we report the effects of contraction intensity on MUNEs with aging. Similar to the current and previous findings in the young,[5,14,29] the S-MUP negative-peak amplitude showed an increase with an increase in contraction intensity in the old men. It seems that irrespective of age there is a failure to record smaller S-MUPs at higher contraction intensities due to a technical limitation in the ability of the DE-STA system to decompose interference patterns of greater complexity.[5] That is, the smaller S-MUPs are lost in the EMG activity of the larger S-MUPs, which increases the relative sampling of larger mean S-MUP amplitudes at higher contraction intensities. In keeping with the size principle, there are increased numbers of larger MUs, and therefore S-MUPs, at higher contraction intensities. As a result of pooling MUs recorded at a variety of contraction intensities, a representative MUNE was extrapolated to an intensity of 15% MVC for both the old and young men. Thus, the use of the same contraction intensity to compare MUNEs across age groups appears to be valid in the SOL, although validity could vary with muscle group and subject age.

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