Age-related changes in the twitch contractile properties of human thenar motor units

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Doherty, Timothy J., and William F. Brown. Age-related changes in the twitch contractile properties of human thenar motor units. J. Appl. Physiol. 82(1): 93–101, 1997.—The purpose of this study was to examine the effects of aging on the contractile and electrophysiological properties of human thenar motor units (MUs). Percutaneous electrical stimulation of single motor axons within the median nerve was used to isolate and examine the twitch tensions, contractile speeds, and surface-detected MU action potential (S-MUAP) sizes of 48 thenar MUs in 17 younger subjects (25–53 yr) and 44 thenar MUs in 9 older subjects (64–77 yr). A wide range of twitch tensions, contractile speeds, and S-MUAP sizes was observed in both age groups. However, older subjects had significantly larger MU twitch tensions and slower MU twitch contraction and half-relaxation times. These changes were accompanied by increased S-MUAP sizes. These findings suggest that the thenar MU pool undergoes significant age-related increase in MU size and slowing of contractile speed. Such adaptation may help to overcome previously reported age-related losses of thenar MUs.

AGING IN HUMANS is associated with decline in strength and atrophy of skeletal muscles (16, 18, 21, 26). These changes may be attributed, in part at least, to losses of motor units (MUs). For example, by using one electrophysiological technique, we recently showed that the numbers of MUs comprising the thenar muscles of healthy subjects between 60 and 80 yr of age were reduced, on average, by about one-half compared with subjects between 20 and 40 yr of age (13). Such an order of magnitude of age-related loss of MUs was similar to previous reports for the thenar muscles (4, 38) and other distal (9, 38) and proximal muscle groups (7, 11, 16).

Other studies have shown significant, although generally less-marked, age-related reductions in the force output of muscles (9, 16, 24, 48). Losses of close to one-half of the normal complement of MUs in skeletal muscles in the elderly may be partially offset by adaptations such as collateral sprouting from surviving motor axons to reinnervate muscle fibers denervated by the loss of their parent motoneuron (3, 5, 31, 32). The presence of such a positive age-related adaptation is supported by the finding of increases in MU action potential size, whether detected with concentric needle electrode, macroneedle electrode, or surface electrodes (7, 11, 13, 22, 31, 41).

Few studies (9, 20, 36) have examined age-related changes in the contractile properties of human MUs, probably because of the formidable technical problems these studies present in vivo. Such studies, however, are important because assessments of the overall force output of muscles or muscle groups may mask differences in the effects of aging on different physiological types and properties of the MUs. The purposes of this study were, therefore, to 1) examine the contractile properties of single thenar MUs as collected with threshold percutaneous stimulation of single motor nerve fibers, 2) look for age-related differences in these properties, and 3) examine whether there were any significant differences in the impact of aging on MUs of differing physiological type.

METHODS

Experimental setup. The thenar muscles were studied, often bilaterally, in 17 younger subjects aged 25–53 yr (mean 35 ± 10 yr), 12 of whom were men, and 9 older subjects aged 64–77 yr (mean 70 ± 3 yr), 4 of whom were men. All subjects were healthy and gave their informed consent. The methods had been previously reviewed by the University of Western Ontario Standing Committee on Human Research.

The electrophysiological techniques for recording the thenar maximum M potential and surface-detected MU action potentials (S-MUAPs) by means of carefully graded electrical stimuli applied through a bipolar percutaneous electrode have all been described in detail by us previously (13, 14). The criteria for accepting a surface-detected potential as that generated by a single MU have also been outlined in detail (1, 13, 14, 30). All electromyographic (EMG) data were collected on an Advantage EMG System (Advantage Medical, London, ON) using custom and commercially available software.

For these studies the subjects were comfortably seated and the outstretched hand and arm were placed on a Plexiglas support attached to a metal plate. The hand was packed in modeling clay and held in place with a wedge-shaped metal bar that applied pressure to the palm without contacting the thenar eminence (Fig. 1). No other stabilization was used because further measures to immobilize the hand or forearm simply made the procedure more uncomfortable without conferring any advantage for resolving the twitches of single thenar MUs.

Force-collection system. Twitch forces exerted by thenar MUs vary widely with respect to their primary vector (43). We, therefore, employed a two-axis force-collection system to measure the force generated by individual thenar MUs in the abduction as well as flexion plane. This enabled the resultant prime vector of the MU to be derived and the associated twitch force to be determined. This was essential because, except for those instances where the presumed location of the MU could be estimated from the electrode detection site where the S-MUAP was maximal, or those few MUs that generated large enough twitches to dimple the skin overlying the MU, it was impossible to predict with accuracy the prime vector for many individual MUs. Earlier attempts to determine the prime force vector for single MUs by searching with
a single-axis system were found to be too tedious and time consuming.

Two force transducers (model FT10, Grass Instruments, Quincy MA; stiffness 0.2 mm/N) were mounted at right angles to each other on adjustable micrometer stages, which allowed each to be precisely positioned independently of the other. Bridge excitation and signal amplification were provided by two separate strain-gauge signal conditioners (Durham Instruments, Pickering, ON; DC 6 kHz, 3 dB down), which had been previously calibrated. The force transducers contacted the comfortably extended thumb at the level of the interphalangeal joint via slightly curved aluminum cups 3 by 10 mm in size, and 0.5 N of passive force was applied in the direction of thumb abduction and flexion (Fig. 1).

Isolation of single MU responses. During the initial search for suitable single thenar motor axons, the median nerve was stimulated at frequencies of ≤1 Hz by using a hand-held bipolar stimulating electrode. The electrode incorporated two saline-soaked felt pads ~5 mm in diameter and 30 mm apart (model 13L36, Dantec) and was used in conjunction with a constant-voltage stimulator (model S48m, Grass Instruments) and stimulus isolation unit (model SIUS).

The search for single MUs was carried out by looking for sites at which a single thenar motor axon could be stimulated along the course of the median nerve between the thenar motor point and the distal forearm. More proximal sites along the course of the median nerve were often unsuitable for finding single thenar motor axons because it was too difficult to find sites in this region where a single thenar motor axon could be found with a stimulus threshold sufficiently below that of any median motor axons supplying forearm muscles. The latter was necessary for the purposes of these studies to avoid distorting the thenar MU twitches by contraction of the forearm muscles.

Criteria for accepting an electrophysiological and force response as generated by a single thenar MU in response to stimulation of the median nerve. We have previously described in detail the electrophysiological criteria required to ensure that single MU responses are obtained by threshold percutaneous stimulation of the median nerve (13, 14). These electrophysiological criteria and the additional criteria required to ensure that the twitch force represented a single thenar MU were as follows.

1) The presence of “all-or-nothing” MUAPs as detected by surface electrodes (and in some instances an intramuscular needle electrode) in response to small increments and decrements in the stimulus intensity delivered to the nerve at the selected site along its course (see Fig. 1, Ref. 14).

2) Successive “all” responses, or S-MUAPs, were identical in shape, size, and latency in response to successive stimuli exceeding threshold, and the S-MUAPs exhibited no fractionation or alternation such as might indicate the presence of two or more thenar motor axons with overlapping thresholds (see Fig. 2; Refs. 13, 14).

3) The all-or-nothing responses of the S-MUAP were matched by all-or-nothing twitch responses in the corresponding MU in response to the same graded changes in the stimulus intensity. This particular criterion, however, could not be reliably depended on as a mandatory selection criterion for all MUs because the small size of some twitches precluded reliable visual identification of their twitch without averaging 5~20 successive responses. Many MUs, however, did generate large enough forces for the twitch response to be sufficiently defined without signal averaging. In these latter instances, the all-or-nothing twitch response of the MU corresponded with the equivalent all-or-nothing S-MUAP (Fig. 2).

4) The excitation threshold of the chosen motor axon was sufficiently separate from that of neighboring thenar motor axons to allow stimulation frequencies as high as 30 Hz or more without exceeding the thresholds of other thenar motor axons. In practice, this meant that the stimulus threshold of the next higher threshold thenar motor axon(s), at a given

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future analysis. Width of 2 Hz to 2 kHz. All data were stored on a hard disk for
whereas the surface EMG was sampled at 5 kHz with a band
split-screen display. The force signal was sampled at 500 Hz,
analog-to-digital converter) and viewed on a four-channel
Averaging was limited to the number of traces required to
reset the baseline to zero just before the delivery of each
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sponse as generated by a single thenar MU in response to
stimulation of the median nerve,

Initially, it was hoped that single raw force responses would
typically 5–20 responses
to maintain isolation of a particular motor axon.

If a site was found meeting all of the above criteria for a
single motor axon and MU, the stimulating electrode
was usually taped in place for the remainder of the studies on
that MU. In some cases, however, it was actually preferable
for the operator to hold and make minor adjustments in the
pressure and position of the stimulating electrode as required
to maintain isolation of a particular motor axon.

Force and EMG data collection. At the gains required to
detect single MU twitch forces, baseline fluctuations related to
respiration, pulse pressure waves, and other movements
often exceeded the size of the MU twitches. These fluctua-
tions were minimized in two ways, based on methods de-
described by Westling et al. (49). The pressure waves associated
with the cardiac pulse were minimized by detection of the latter
by using an infrared finger pulse monitor from which a
trigger pulse was delivered to the stimulator after a delay of
50–150 ms. In this way, the contractile response of the MU
was collected in the cardiac pulse-free period between succes-
several trials. Movement related to respiration was dealt
wascollectedinthecardiacpulse-freeperiodbetweensucces-

After isolation of a stable single motor axon as outlined in
Criteria for accepting an electrophysiological and force re-
sponse as generated by a single thenar MU in response to
stimulation of the median nerve, typically 5–20 responses
were ensemble averaged to obtain the MU twitch force.
Initially, it was hoped that single raw force responses would
be acceptable, but despite the above measures the back-
ground noise level relative to the small size of many of the
twitches mandated the use of averaging for most MUs.
Averaging was limited to the number of traces required to
produce a stable twitch response.

Force and EMG signals were collected on-line (12-bit
analog-to-digital converter) and viewed on a four-channel
split-screen display. The force signal was sampled at 500 Hz,
whereas the surface EMG was sampled at 5 kHz with a band
width of 2 Hz to 2 kHz. All data were stored on a hard disk for
future analysis. Channel 1 sampled only the stimulus arti-
fact, which served as a triggering source to generate time-
tooked delayed sweeps of channels 2–4. Channel 2 displayed the
surface-detected EMG, and channels 3 and 4 displayed the
abduction and flexion components of the twitch, respec-
ively (Fig. 2). Additionally, the unaveraged surface EMG
signal was monitored on a storage oscilloscope to ensure that
the same single MU as indicated by its unique S-MUAP was
evoked with each stimulus. If an F response occurred, the
trial was discarded and restarted to avoid distortion of the
twitch by the additional force contribution of the recurrent
discharge of the MU.

Force data analysis. The force signals were analyzed
on-line by a separate computer algorithm. The algorithm
derived the resultant composite twitch force from the abduc-
tion and flexion force components. The peak twitch force
(mN), contraction time (CT; time in ms from onset of force
response to peak twitch tension), and half-relaxation time
(RT, ½; recovery time in ms from peak force to a value one-half
of the peak) were determined by a computer algorithm from
the resultant composite force record.

EMG data analysis. The negative peak areas (µV·ms) of
the associated S-MUAPs were determined by a computer
algorithm. As well, S-MUAP negative peak areas were normal-
ized to the size of the maximum M-potential negative peak
area as detected with the same electrode configuration.
Finally, after collection of the force response, repeated stimulii
(often >100) were delivered to the motor axon in an attempt
to evoke an F response. When an F response occurred, the
motor axon conduction velocity (CV) was calculated as de-
scribed previously (15).

Values are means ± SD throughout the text. Comparisons
between mean values were made with two-tailed t-tests,
and relationships between associated variables were analyzed
with linear regression.

RESULTS

From examination of the median innervated thenar
muscles of 17 younger subjects, a total of 48 MUs were
collected from which satisfactory contractile and electro-
physiological data could be derived. The yield per
subject ranged from 1 to 5 MUs, with a mean yield of
2.8 ± 1.2. From 9 older subjects, 44 MUs were studied
with the yield per subject varying from 1 to 7 MUs. The
mean yield in the latter subjects was 4.8 ± 1.8. The
results for younger and older subjects are summarized in
Table 1.

Characteristics of MUs from younger subjects. Figure
3 illustrates the MU twitch records and associated
S-MUAPs for five representative MUs from two youn-
ger subjects. The twitch tensions varied widely from 1.5

Table 1. Contractile and electrophysiological data
of motor units

<table>
<thead>
<tr>
<th></th>
<th>Younger Subjects (n = 48)</th>
<th>Older Subjects (n = 44)</th>
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<tbody>
<tr>
<td>Force, mN</td>
<td>8.8 ± 7.4 (1.5–33.2)</td>
<td>13.4 ± 10.4 (2.8–54.8)*</td>
</tr>
<tr>
<td>CT, ms</td>
<td>49.5 ± 11.5 (28–72)</td>
<td>56.7 ± 14.0 (30–93)†</td>
</tr>
<tr>
<td>RT, ½, ms</td>
<td>55.2 ± 22.2 (18–120)</td>
<td>69.3 ± 27.6 (28–134)^</td>
</tr>
<tr>
<td>S-MUAP, µV·ms</td>
<td>394 ± 325 (30–1208)</td>
<td>459 ± 458 (16–2,012)†</td>
</tr>
<tr>
<td>Max M, mV·ms</td>
<td>45.8 ± 11.3 (15.7–64.8)</td>
<td>32.2 ± 8.4 (18.1–49.9‡)</td>
</tr>
<tr>
<td>%Max M</td>
<td>0.91 ± 0.75 (0.07–2.56)</td>
<td>1.59 ± 1.89 (0.04–10.8‡)</td>
</tr>
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</table>

Values are means ± SD with ranges in parentheses; n, no. of motor
units. CT, contraction time; RT, ½, half-relaxation time; S-MUAP,
surface-detected motor unit action potential; Max M, maximum
compound muscle action potential; %Max M, S-MUAP size as percent-
age of each subject's maximum compound muscle action potential
size. Younger subjects vs. older subjects: *P < 0.05; †P < 0.01; ‡P <
0.001; §not significant.
to 33.2 mN with greater numbers of MUs generating small twitch forces (Fig. 4). MU twitch CT values ranged from 28 to 72 ms, and the RT\textsubscript{1/2} values ranged from 18 to 120 ms (Figs. 5 and 6).

S-MUAP negative peak areas varied widely in size from 30 to 1,208 µV·ms (Fig. 7). The distribution of S-MUAP sizes was similar to the distribution of MU twitch forces, there being relatively greater numbers of responses generating smaller S-MUAPs and forces.

Fig. 3. Representative thenar motor unit (MU) twitches and their associated S-MUAPs from 2 younger subjects. A: force. B: S-MUAP. S-MUAPs are the lowest threshold all-or-nothing potentials in response to threshold stimulation of the median nerve around the wrist. Twitches represent ensemble-averaged (5–20 sweeps) force records corresponding to S-MUAPs (vertical calibration bar for force, 2 mN).

Fig. 4. Distribution of thenar motor unit twitch forces in younger (A) and older subjects (B) (see Table 1 for values).

Fig. 5. Distribution of thenar motor unit twitch contraction times (CT) in younger (A) and older subjects (B) (see Table 1 for values).
MU twitch force was significantly correlated with S-MUAP negative peak area ($r = 0.582; P < 0.001$).

In 15 of the 48 MUs, an F response was evoked and the CV of the MU was calculated. CVs ranged from 49 to 67 m/s, with a mean value of 59 ± 4 m/s. CVs were not significantly correlated with either the twitch force, CT, or RT$_{1/2}$. Furthermore, twitch force was not significantly correlated with CT or RT$_{1/2}$. However, the CT and RT$_{1/2}$ were significantly correlated ($r = 0.566; P < 0.001$).

Comparison between MU contractile and electrophysiological properties in younger and older subjects. As was the case in younger subjects, MUs in older subjects exhibited a wide range in their twitch tensions and a relatively greater preponderance of MUs generating smaller twitch tensions (Fig. 4, Table 1). In older subjects, however, the distribution was shifted to the right and the mean MU twitch force was significantly greater than that for the younger subjects (34%; $P < 0.05$). The CT and RT$_{1/2}$ of MUs in older subjects exhibited widely ranging values with somewhat greater variability in twitch duration compared with the younger subjects (Figs. 5 and 6). On average, the time course of the MU twitch was prolonged, as indicated by the modest yet significantly increased mean CT ($P < 0.01$) and RT$_{1/2}$ ($P < 0.01$) (Table 1).

S-MUAPs from older subjects, as for the younger subjects, exhibited a wide range of negative peak areas with a positively skewed distribution (Fig. 7). The mean S-MUAP size did not significantly differ, possibly because of the small sample size and wide range of values in both age groups. However, when the S-MUAP sizes were normalized to their respective maximum M-potential negative peak area, the mean value for older subjects was significantly larger compared with the younger subjects (43%; $P < 0.05$).

Only 6 of 42 MUs in older subjects were found to have an F response, despite the delivery in each case of ≥100 stimuli. This subset of data was considered too small to analyze statistically with regard to age-related changes in MU axonal CVs and contractile properties (but see Ref. 15).

As for the younger subjects, there were no significant correlations between MU force and either CT or RT$_{1/2}$ in older subjects. CT and RT$_{1/2}$, however, were significantly related ($r = 0.566; P < 0.001$) as were MU force and S-MUAP size ($r = 0.404; P = 0.007$).
DISCUSSION

In this study, the electrical and contractile properties of single thenar MUs in younger and older subjects were studied. It proved possible, by using carefully graded percutaneous stimulation, to excite between one and five single median motor axons in most subjects and measure the size of the associated MU twitch responses and S-MUAPs. However, before our findings in younger and older subjects are discussed, the underlying assumptions and potential biases in our method of collecting single MUs need to be addressed.

Were the criteria for single MUs applied in this study sufficiently rigorous to justify acceptance of their twitches and associated S-MUAPs as generated by single MUs? Previous studies in both our own and other laboratories have shown that it is entirely possible to stimulate a single motor axon without stimulating other motor axons lying within a motor nerve (1, 2, 4, 8, 9, 13, 14, 30, 39, 49). This may be accomplished by means of a stimulating electrode applied percutaneously or through the insertion of a microelectrode directly into the nerve trunk. To successfully stimulate a single motor axon by using a surface electrode requires the following: 1) the ability to carefully grade and control the stimulus intensity applied to the nerve, 2) an often painstaking search for a location along the course of the nerve at which a single motor axon can be excited with a threshold sufficiently below that of other motor axons to allow the chosen motor axon to be confidently stimulated without fear of exciting neighboring motor axons, and 3) holding the electrode steadily enough for the MU to be studied.

At such a carefully chosen site, repeated stimuli delivered to the axon at threshold will either fail to evoke any electrical or mechanical activity, the “nothing” response, or an “all” response signalled by the appearance of the S-MUAP and the corresponding twitch generated by the MU. Furthermore, successive stimuli with an intensity that exceeds the threshold for only the chosen motor axon will evoke successive identical S-MUAPs, which are constant in shape and size throughout the range of stimulus intensities employed in the study (Fig. 2; Refs. 13, 14).

In the present study, additional evidence supporting that a single motor axon had been stimulated was the finding that the S-MUAPs generated by the direct and F response were identical in shape and size. However, because not all MUs produced an F response, despite in many cases the delivery of hundreds of successive stimuli to the single motor axon, acquiring an F response was not an absolute criterion for the acceptance of an S-MUAP as representing the potential generated by a single MU. Finally, helpful, but not mandatory, to the determination of single MU status was the presence of a clearly defined all-or-nothing twitch response generated by the putative MU in response to single stimuli. The reason for the latter was the fact that the single twitch responses of some thenar MUs were simply too small relative to the noise level of our force-collection system to be clearly defined without resorting to signal averaging. However, we felt it was entirely reasonable to assume that signal-averaged force responses, corresponding to the rigorously defined all-or-nothing S-MUAPs, indeed represented the twitches of single thenar MUs.

Was the sample of MUs representative of the true physiological range of MUs in the thenar muscles? Despite the small yield of MUs per subject, provided there was no systematic selection bias toward motor axons of any particular physiological type or CV, the entire sample should have faithfully approximated the range of contractile characteristics, S-MUAP sizes, and CVs of the whole population of MUs. That there was no such systematic bias is suggested by the wide range of twitch tensions, contractile speeds, and CVs of the MUs in this study. In addition, the distributions and sizes of the thenar S-MUAPs and CVs were similar to previous studies of the same muscle (12, 13, 15, 42–44).

The studies of Thomas et al. (43) and Westling et al. (49) of single thenar MU contractile properties provides the most directly comparable results with which to compare our findings. Their force-collection system (43, 49) was similar to that employed in the present study, and the MUs were collected by stimulating single motor axons within the median nerve trunk. They reported a range of MU twitch tensions of 2.9–34.0 mN with a mean value of 11.3 ± 8.2 mN, values very similar to our own range of 1.5–33.2 mN and mean of 8.8 ± 7.4 mN for younger subjects. As well, the range of values of CT (35–80 ms) and RT1/2 (25–108 ms) in their study were very similar to our findings for CT (28–72 ms) and RT1/2 (18–120 ms).

On the basis of the foregoing and other previously published evidence (1, 13–15, 38) we, therefore, feel that we were able to successfully isolate and examine the physiological properties of single thenar MUs without any apparent bias toward a particular type of MU. It must be admitted, however, that we do not know what factors apparently govern the fortuitously low threshold of some motor axons at certain sites of stimulation (17). Nevertheless, whatever those factors might be, they apparently have little to do with the CVs or contractile properties of their associated MUs.

The most important difference between the study of Thomas et al. (43) and the present study was methodological in that they employed intraneural microstimulation to excite single thenar motor axons, whereas we used percutaneous stimulation. The latter, while at first glance appearing less refined than intraneural microstimulation, is nonetheless capable of stimulating single thenar motor axons and carries the added attractive prospect in some cases of being able to find and longitudinally follow the same MU in serial studies over many weeks and months (14). The method of percutaneous stimulation of single motor axons offers investigators the possibility of examining the influence of training and other interventions on specified single MUs. Studies of this nature are currently underway in our laboratory.
What were the relationships between the CV and contractile properties of thenar MUs? No significant correlations were found between the CVs of thenar motor axons and either the twitch tensions or contractile speeds of the corresponding MUs. Additionally, there was no correlation between contractile speed and twitch tension of the MUs. Thomas et al. (43), similarly, found no significant correlation between axonal CV and MU twitch or tetrode tension and only weak correlations between CV and contraction rate measures. Given the apparent lack of any strong correlation in these studies among contractile speed, twitch tension, and motor axon CV, previous assumptions concerning these relationships based largely on studies in other species may have to be reexamined for their relevance in humans.

Age-related changes in MU contractile and electrophysiological properties. The mean MU twitch tension was significantly increased in the elderly. This was accompanied by a shift in the distribution toward a greater proportion of MUs generating larger twitch tensions (Fig. 4). For example, in younger subjects, close to one-third of the MUs generated twitch tensions of ≤4 mN and >50% of the twitch tensions were ≤8 mN. On the other hand, in the older subjects, <10% of the MUs generated twitch tensions of ≤4 mN and only one-third of the total generated twitch tensions of ≤8 mN. There was also a greater proportion of MUs generating twitch tensions >16 mN in the older subjects.

Overall, the age-related increase in MU twitch tension was on the order of 34%. This value was similar to the 37% increase in the mean thenar S-MUAP size determined by multiple-point stimulation (13) and the 39% increase in the mean size of thenar S-MUAPs drawn from F responses (15). An earlier study had shown a significant yet less-marked age-related increase (23%) in the mean size of biceps-brachii and brachialis S-MUAPs (16). The extent to which these discrepancies reflect true differences in the effects of brachialis S-MUAPs (16). The extent to which these discrepancies reflect true differences in the effects of aging on proximal and distal muscle groups as opposed to any methodological differences in the collection and detection of S-MUAPs is unknown (31).

Earlier studies of the contractile properties of whole muscles (or muscle groups) in the elderly have, for the most part, shown increases in the duration of the twitch response (9, 10, 24, 47, 48). The CT and RT1/2 observed in the elderly could be explained in one of several ways. For example, there may be a shift in the relative proportion of slow- and fast-twitch MUs, with a preponderance of the former. Such a shift, in turn, may reflect greater losses of fast-twitch MUs or the possible conversion of at least some of the fast-twitch MUs to twitch speeds more characteristic of slow-twitch MUs. For example, in the aged rat, Pettigrew and Gardiner (37) reported reduced tetanic tensions and significantly prolonged CTs in the plantaris muscle accompanied by losses of MUs on the order of 40% and an increase in the ratio of slow-twitch MUs. Similarly, Kanda and Hashizume (23) reported a significant age-associated reduction in the mean tetanic tension of fast-fatigable, fast-intermediate, and fast-fatigue-resistant MUs in the face of substantial increases in the mean tetanic tension of slow-twitch MUs. Taken together, the foregoing studies in the rat suggest that there is an age-associated reorganization of the MU pool characterized by selective losses of fast MUs and increases in the relative numbers of MUs with slow and transitional properties. However, the balance of evidence from studies of human vastus lateralis muscle using histochemical techniques suggests that fiber type proportions are not significantly altered with aging (28).

Whether such changes as occur with aging in the rat explain the effects on the contractile characteristics of human muscles is not clear on the basis of this present study. Certainly there is abundant physiological and some anatomic evidence for significant losses of functioning MUs on the order of one-third to one-half in the later decades of life in healthy adults (4, 7, 9, 13, 16, 18, 19, 41, 46). As well, reductions in the maximum CVs have been reported in various motor nerves in humans (9, 45). However, recent evidence suggests that the latter reductions in maximum motor CVs may not reflect so much a selective loss of the more rapidly conducting motor axons but a more or less uniform slowing of the CVs of all motor nerve fibers with aging (15, 33).

There certainly was no indication in the present study for selective losses of the fast twitch MUs. Older subjects appeared to maintain the full range of contractile speeds with regard to both CT and RT1/2 compared with the younger adults. The difference between MUs in the young and the elderly was characterized by a shift in the distribution toward a greater proportion of MUs exhibiting prolonged CT and RT1/2. However, there is no way, based on these data alone, of determining whether this shift reflected preferential losses of fast-twitch MUs as shown in the rat or random losses of MUs and slowing of the contractile speeds of all MUs regardless of their physiological type.

In addition, the rates of CT and RT1/2 of the MU are dependent on the duration of the active state of its constituent fibers. The duration of the active state in turn is dependent on the concentration of calcium around the contractile filaments (29). Evidence of damage to the sarcoplasmic reticulum (SR) with advanced age has been provided both in human vastus lateralis muscles (25) and in rat muscle (27), in which a type II fiber-specific decrease in SR volume, rate of calcium uptake, and calcium pump activity has been reported.

Whatever the underlying mechanism for the slower contractile speeds of MUs in the elderly, both the present study and the few previous studies of the physiological properties of single MUs in the elderly all point toward an increase in the average MU twitch tension coupled with increases in the CT and RT1/2 of MU twitch contractions (9, 20, 36). These findings provide strong evidence for age-associated remodeling of the motor unit pool after significant loss of α-motoneurons.

The reported increases in the contractile speeds of single MUs in the elderly may be linked to previously...
reported reductions in MU firing rates with aging in both proximal and distal muscles (2, 22, 35, 40). Prolonged CT and RT 1/2 may be a useful compensatory mechanism enabling MUs in elderly subjects to achieve fused tetanic forces at lower firing frequencies. In this fashion, less central drive would be required to reach a given contractile force. Indeed, Narici et al. (34) reported that the adductor pollicis muscle of older subjects produced greater relative forces at lower stimulus frequencies compared with younger subjects. However, this increase in force output per MU may be at the expense of fine motor control (20), and slower MUs might hinder the ability to produce large forces rapidly, such as needed in avoiding a potential fall (47, 48).

In summary, we believe based on these and previous studies that percutaneous electrical stimulation of single median motor axons provides an alternative to intraneuronal microstimulation as a means of examining the contractile characteristics and CVs of single MUs. Surface stimulation offers the advantage of being less invasive and the potential of studying the same MU longitudinally. These advantages are possibly offset by the relatively few numbers of MUs meeting the inclusion criteria in individual subjects.

Our findings have shown age-related increases in thenar MU twitch tension and slower MU contractile speeds. Taken together with previous findings of significant losses of MUs (7, 9, 13, 16, 39), the increases in force output and slower contractile speeds probably represent positive adaptations to the reduced MU numbers. The question of whether these adaptations affect all MUs to the same extent regardless of their original physiological type was not resolved in this study.

A continuum of twitch tensions, contractile speeds, S-MUAP sizes, and axonal CVs was observed in our study with no clear division of MUs into subgroups based on their physiological characteristics. The distributions of MU twitch tensions and S-MUAPs were skewed toward a preponderance of smaller MUs in both younger and older subjects. Finally, no significant correlations were found between the CVs of thenar motor axons and the twitch tensions or contractile speeds, a finding at variance with studies in other species but consistent with some recent human studies (43, 49).

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