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Effects of Aging on Motor-Unit Control Properties

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Erim, Zeynep, M. Faisal Beg, David T. Burke, and Carlo J. De Luca. Effects of aging on motor-unit control properties. *J. Neurophysiol.* 82: 2081–2091, 1999. It was hypothesized that the age-related alterations in the morphological properties of a motor unit would be accompanied by modifications in the control aspects of the motor unit, as either an adaptive or compensatory mechanism to preserve smooth force production. In specific, the objective of the study was to investigate the age-related alterations in the concurrent firing behavior of multiple motor units in the first dorsal interosseous (FDI) muscle in isometric contractions at 20 and 50% of the subject's voluntary contraction level. Analysis of the data collected from 10 young (24–37 yr of age) and 10 elderly (65–88 yr of age) subjects led to three novel observations regarding the firing behavior of aged motor units. *1*) Among elderly subjects, there is a decrease in the common fluctuations that are observed among the firing rates of motor units in the young. *2*) The relationship observed between the firing rate and recruitment threshold of young subjects is disturbed in the elderly. Although in young subjects, at any point in a given submaximal contraction, earlier recruited motor units have higher firing rates than later-recruited units; in aged subjects this dependency of firing rate on recruitment rank is compromised. *3*) The progressive decrease observed in the firing rates of concurrently active motor units in constant-force contractions in the young is not seen in the aged. In addition to these original findings, this study provided support for earlier reports of *1*) decreased average firing rates probably reflecting the slowing of the muscle, *2*) a shift in recruitment thresholds toward lower force levels in line with the shift toward type I fibers, and *3*) multiphasic action potential shapes indicative of the reinnervation process that takes place during aging. Taken as a whole, these findings indicate significant age-related modifications in the control properties of human motor units.

INTRODUCTION

It is well-known that the physiological characteristics of human nerves and muscle fibers change with age. The vast bulk of research in this area has been on identifying the changes in the morphological (Kanda and Hashizume 1989), physiological (Roos et al. 1997), and histochemical (Ansved and Larsson 1995) properties of the motor unit (MU) with age. In light of the significant changes in the properties of the elements of a motor unit, it can be hypothesized that the control aspects of the motor unit would be modified as an adaptive or compensatory mechanism to preserve force production. Indeed, the firing rates of aged motor units were found to be lowered in several studies (Howard et al. 1988; Nelson et al. 1984; Newton et al. 1988; Soderberg et al. 1991). Other studies reported decreased firing rates specifically at high level con-

tractions (Kamen et al. 1995). Another study on the first dorsal interosseous (FDI) reported an altered mode of recruitment/derecruitment in the elderly (Kamen and De Luca 1989). In contrast, Galganski et al. (1993) reported no age-related change in the firing behavior of FDI motor units during a threshold task. Apart from these few studies, there is little published data on the control aspect of the motor unit, especially at higher force levels.

The Precision Decomposition technique (De Luca 1993; LeFever et al. 1982) allows accurate identification of the firing times of motor units enabling investigation of the firing behavior of several concurrently active motor units as a function of time. The objective of this study was to investigate the age-related alterations in the firing behavior of concurrently active human motor units in the FDI muscle at force levels that were significantly different from threshold [20 and 50% maximal voluntary contraction (MVC)], using the accuracy offered by the Precision Decomposition technique. At these force levels, especially at 50%MVC, it is possible to observe a motor unit sample that is representative of the whole population.

METHODS

Experimental design

SUBJECTS. Data were collected from a total of 20 subjects. The group of 10 subjects 20–37 yr of age (30.2 ± 5.66 yr, mean $\pm$ SD) were classified as "young," and the group of 10 subjects 65–88 yr of age (76.9 ± 6.56 yr) were classified as "elderly." The elderly subjects were screened by a practicing physiatrist for neuromuscular disorders that may interfere with the study. Local and institutional review board approval was obtained, and all the subjects gave informed consent. Force and myoelectric data were collected from the FDI muscle of the dominant hand.

ISOMETRIC FORCE RECORDINGS. The hand of the subject was immobilized by placing it in a special mold so that the FDI was constrained to contract isometrically. The force of isometric abduction and flexion were measured by placing a high-stiffness strain-gauge force transducer against the proximal interphalangeal joint of the index finger. The force signals were amplified and filtered (DC-300 Hz) before acquisition and storage on a PC as well as being recorded on instrumentation tape for backup.

PROTOCOL. The MVC was acquired by instructing the subject to maximally abduct the index finger and measuring the force produced. This was repeated three times, and the maximum force measured was taken as the abduction MVC. Subsequently, the same procedure was repeated for the flexion direction, and the flexion MVC was determined. Flexion force was recorded (as a percentage of the flexion MVC) to ensure that the subject was performing the prescribed task of contracting only in the abduction direction.

The subjects were asked to trace a trapezoidal trajectory on the computer screen by abducting the index finger with visual feedback

on force. The plateau of the trapezoidal trajectory was scaled to the subjects' MVC, and the ramp parts of the trajectory had a slope of 10%-MVC per second. The subjects practiced a few short trials at 20 and 50%-MVC to familiarize them with trajectory tracing. When they were able to follow the trajectory smoothly, the needle electrode was inserted in the belly of the muscle.

Myoelectric data were acquired while the subject traced the trajectories at plateau levels of 20 and 50% of the MVC. The duration of the force plateau in these trials was 60 and 20 s, respectively. The set of contractions was repeated, with a minimum rest period of 3 min between the trials. Before beginning each trial, the needle electrode position was checked at a low level contraction of ~10%-MVC to ensure the presence of three or four large and distinct motor-unit action potentials in the detected intramuscular electromyographic (EMG) signal.

MYOELECTRIC SIGNAL RECORDINGS AND ANALYSIS.   The specially designed 25-gauge quadrifilar needle electrode used to acquire myoelectric data carries in its bore four pickup wires (cross-sectional diameter 50 μm), which are exposed from a side port on the cannula and separated by 200 μm. The three differential pairs of intramuscular signals (band-pass filtered 1–10 kHz) derived from these four pickup surfaces were recorded in addition to the electrical activity detected by the cannula of the needle with respect to the reference (band-pass filtered 10 Hz to 1 kHz). The surface EMG signal was recorded using a bipolar surface electrode (band-pass filtered 10 Hz to 1 kHz). A moistened velcro strap placed around the forearm near the elbow and an electrode with a gel interface placed on the middle finger served as reference electrodes.

The intramuscular EMG signals were resolved into the individual motor-unit firing trains using the Precision Decomposition technique (De Luca 1993; LeFever and De Luca 1982; LeFever et al. 1982; Mambrito and De Luca 1984). This technique uses template matching, template updating, firing probabilities, and superposition resolution to identify the individual firing times of the motor unit with up to 100% accuracy (Mambrito and De Luca 1984). Operator inspection of the identified motor-unit action potentials was carried out on the decomposed signal train to verify the firing instances of the motor units visually and correct any misidentifications.

Data analysis

DETERMINATION OF CONSTANT FORCE INTERVAL.   To ensure a common basis for comparison of motor-unit firings, a 5-s-long stable force interval was determined for each trial in which the force at any instant in the interval was within $\pm 10\%$ of the mean force in the interval, and the coefficient of variation (CV) of force was <0.4 over this period. Average firing rates and cross-correlation functions between mean firing rates were calculated over the first such stable force interval.

MOTOR-UNIT PARAMETERS.   The *recruitment threshold* of a motor unit was calculated by averaging the force over 15 samples (corresponding to a window of 7.5 ms) beginning at the first discharge time of the motor unit. The continuous *mean firing rate* of a motor unit was obtained by passing a Hanning window of duration ranging from 0.4 to 2 s over an impulse train consisting of the discharge times of the motor unit. The *average firing rate* was defined as the average of the continuous mean firing rate signal in the stable force interval. The *firing rate slope* was calculated as the slope of the regression line fit to the mean firing rate signal in the region starting from where the force and mean firing rates stabilized at the target level to the end of the force plateau. The *mean* and *standard deviation of the interpulse interval* were calculated in the same stable force region, and the *coefficient of variation of the interpulse interval* was defined as the ratio of the standard deviation of the interpulse interval to the mean interpulse interval. The *initial firing rate* was calculated by inverting the average of the first three interpulse intervals corresponding to the

first four firing instances of the motor unit. The choice of four spikes represents a compromise between reducing the variance of the estimate and capturing transient changes in the firing rates, given the high instability of motor-unit firings at recruitment. The *coefficient of variation of force* in a given interval was defined as the ratio of the standard deviation of the force samples to the mean of the force signal in the interval.

RESULTS

Data from a total of 231 motor units were acquired and analyzed during isometric contractions at 20% (69 motor units from the young, 68 from the elderly) and 50%-MVC (43 motor units from the young, 51 from the elderly) force levels.

Interaction among firing rates of concurrently active motor units

It has been proposed that motor units of a given motoneuron pool respond to a "common drive" (De Luca et al. 1982b; De Luca and Erim 1994; Erim 1992) and that the response of an individual motor unit is prescribed by its inherent drive/firing rate characteristics (Erim et al. 1996). The common fluctuations observed in the mean firing rates of concurrently active motor units in healthy, young subjects were attributed to the fluctuations in this common drive to the motoneuron pool. In data collected from young subjects in this study, common fluctuations were consistently observed in mean firing rates at both the 20% and the 50%-MVC levels. Figure 1, *A* and *B,* displays the firing behavior of young motor units at two contraction levels. In addition to the common firing rate fluctuations, the *top panel* of the figure exemplifies other collective firing properties of motor units, which will be discussed. In most aged subjects and in most of the time during the contractions, the common fluctuations in the mean firing rates of motor units were found to be decreased as seen in Fig. 1, *C* and *D*. Note that decreased commonality in MU firing rates is also seen in Figs. 3 and 4, where in addition to the out-of-phase behavior of fluctuations, motor units even exhibited different trends (some increasing at the same time as others decreasing) in their firing rates.

To study the commonality of firing rate fluctuations in the elderly, the pair-wise cross-correlation of the dc-removed mean firing rates of concurrently active motor units was calculated over the 5-s constant force interval. The cross-correlation values obtained from a young and elderly subject are shown in Fig. 2. The cross-correlation values in the elderly are reduced as is evident in Fig. 2*B,* and random phase values between the firing rates are observed. In performing statistical comparison of the common drive behavior in the two age groups, the cross-correlation function was calculated between the mean firing rates of all the motor units observed in a given contraction. This resulted in 146 motor unit pairs in the young and 182 pairs in the elderly group. Because there was no effect ($P > 0.05$) of force level on cross-correlation peak values, the peak cross-correlation values obtained at 20 and 50%MVC levels were grouped together within each age group. The group means $\pm$ SD were 0.49 ± 0.16 for the young, and 0.43 ± 0.14 for the aged group. Because the distribution of the peak values did not conform to a normal distribution, the nonparametric analogue of the two-sample *t*-test, the Mann-Whitney *U* test, was used to compare the two age groups. The hypothesis that
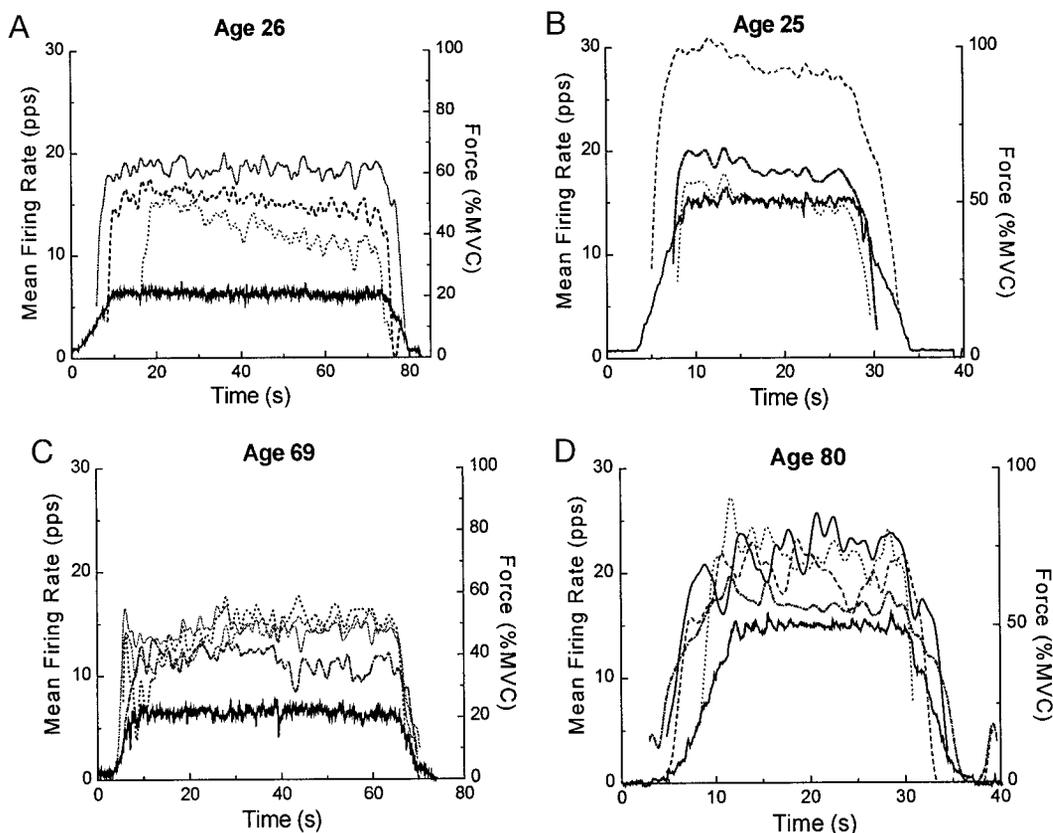
FIG. 1. Mean firing rate curves of concurrently active motor units in 2 young (*A* and *B*) and 2 aged (*C* and *D*) subjects at 20% (*A* and *C*) of maximal voluntary contraction (MVC) and 50% (*B* and *D*) of MVC. The mean firing rates of motor units (the left *y*-axis) as well as the force (the right *y*-axis) at which they were observed are plotted on the same time scale. The mean firing rates were obtained by passing a Hanning window of 2-s duration over an impulse train corresponding to the firing instances of each motor unit.

the two groups had the same distribution was rejected at $P < 0.005$ level of significance. Although the group means appear to be close, the *distribution* of the cross-correlation peak values were different. For instance, in the young 48% of the pairs had peak values >0.5, whereas in the aged only 30% of the pairs had peak values above 0.5. In fact, this difference in distributions is what is captured by the Mann-Whitney test, with the high number of samples available for both groups yielding a high power for the comparison. The location of the peak values, or the delay between the mean firing rates of motor units (0.16 ± 0.28 s for the young, and 0.23 ± 0.31 s for the aged group) were also found to be different at $P < 0.005$ using the Mann-Whitney test. Increased delays and increased variability in delay are to be expected from the reinnervation

process, which alters the distance the action potentials travel along the neurons that have picked up orphan fibers.

Firing rate–recruitment threshold dependence

Another significant property displayed by concurrently active motor units in healthy, young subjects is the inverse relationship between their firing rates and recruitment thresholds (De Luca et al. 1982a; De Luca and Erim 1994; Erim et al. 1996; Person and Kudina 1972). This relationship manifests itself as a nestling of the mean firing rate curves within one another, with the earlier recruited motor units achieving a higher firing rate than the ones recruited subsequently, resulting in the term "onion skin phenomenon" (De Luca and Erim
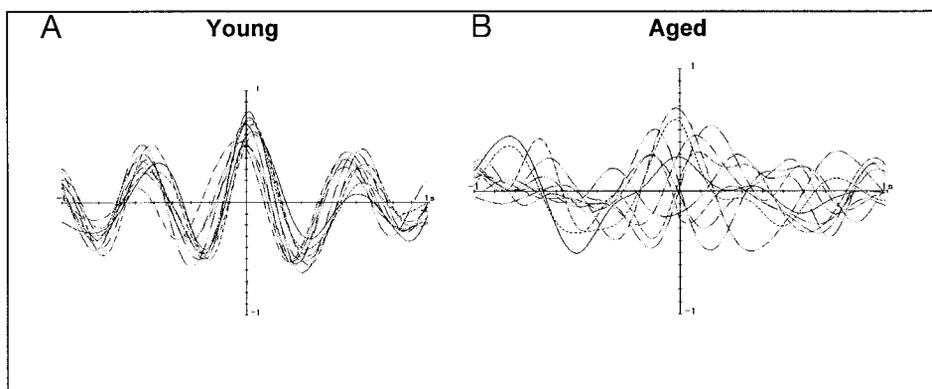

FIG. 2. Cross-correlation of continuous mean firing rates of concurrently active motor units for a young (*A*) and aged (*B*) subject in a 5-s interval. Each line denotes the cross-correlation function of the continuous mean firing rates for a pair of motor units. Cross-correlations were obtained after the dc components were removed from the mean firing rate signals to study the correlation specifically among the fluctuations.
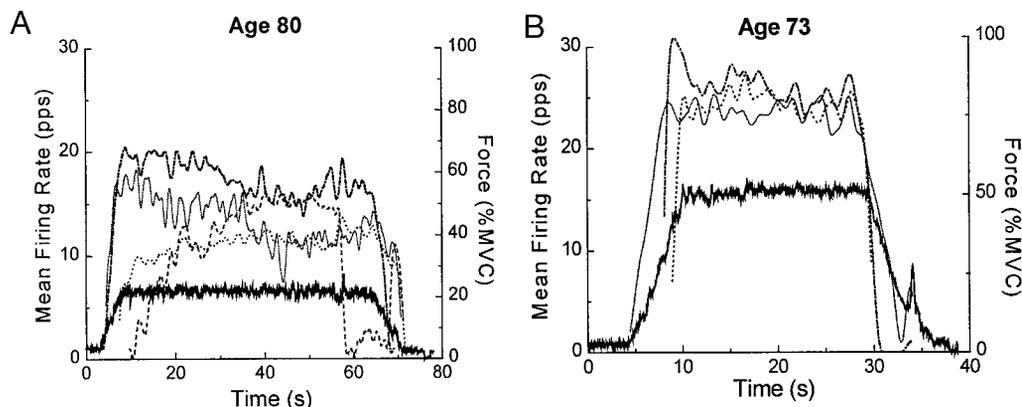
FIG. 3. "Cross-over" of mean firing rate curves of motor units observed in the elderly. The later recruited motor units reach a higher firing rate than those recruited earlier. The firing rate curves from 2 elderly subjects are shown here at 20%-MVC (*A*) and 50%-MVC (*B*) force levels.

1994). In the elderly, the "onion skin" behavior was disrupted in almost all the trials with the mean firing rate curves of the later recruited motor units "crossing over" the mean firing rate curves of the earlier recruited motor units. Figure 3 shows this altered firing behavior in the elderly subjects at the two force levels studied. "Cross-over" is also evident in the *bottom panel* of Fig. 1 and in Fig. 4.

To quantify the extent of the violation of the onion skin rule in the elderly, motor units observed from a given subject were pooled for each contraction level. Regression lines were fit to sample points representing the recruitment threshold and average firing rate of each motor unit identified for the subject at a given force level. Although due to the small sample sizes statistical significance for the regression fit was reached only a quarter of the time, for all of the young subjects (100% of the subjects at both force levels), the slope of the regression line was negative, indicating the onion skin phenomenon. For the elderly subjects, at 20% of MVC 56%, and at 50% of MVC 50% of the subjects had negative slopes, whereas the rest of the subjects displayed positive slopes indicating violation of the onion skin phenomenon.

It is well-known that in the young, the order of de-recruitment of motor units is the reverse of the order of recruitment (see Fig. 1). In the elderly, the same order of recruitment and de-recruitment was noted to be preserved in almost all the cases, i.e., the motor units that were recruited later were de-recruited earlier.

Firing rate trends during sustained contractions

During 8–15 s constant-force contractions in young subjects, the firing rates of motor units gradually decrease with time and the rate of decrease is positively correlated to the recruitment threshold of the motor unit (De Luca et al. 1996). This behavior was observed in the data collected from the young subjects in this study (see Fig. 1, *top panel*). In the data collected from the elderly, few motor units decreased their firing rates with time during the constant force plateau, whereas other concurrently active motor units increased or maintained their mean firing rates as seen in Fig. 4. Note the increasing trend after the first 20 s following the decreasing trend in the mean firing rates in Fig. 4*A*. Firing rate trends in different directions among concurrently active motor units are also seen in the *bottom panel* of Fig. 1 and in Fig. 3. In comparing firing rate trends, we used the slopes of the regression lines fit to mean firing rate signals. In agreement with our previous findings, firing rate drops were significantly higher at the higher force level for both age groups ($P < 0.005$). As the distribution of firing rate slopes did not conform to a normal distribution ($P > 0.05$), the nonparametric Mann-Whitney U test was used to compare the age groups. For the 20% MVC contractions, there was no statistically significant difference ($P > 0.05$) between the two age groups (-0.050 ± 0.049 pps^2 for the young; -0.040 ± 0.049 pps^2 for the aged). However, at 50% MVC, there was a significant difference at $P < 0.005$
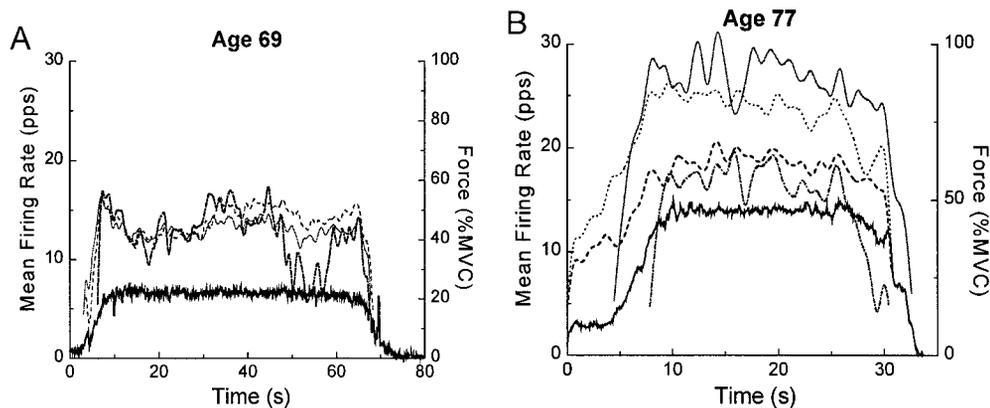

FIG. 4. Mean firing rate curves for 2 elderly subjects at 20%-MVC (*A*) and 50%-MVC (*B*) force levels showing an absence of decrease in the firing rates at a sustained force level.
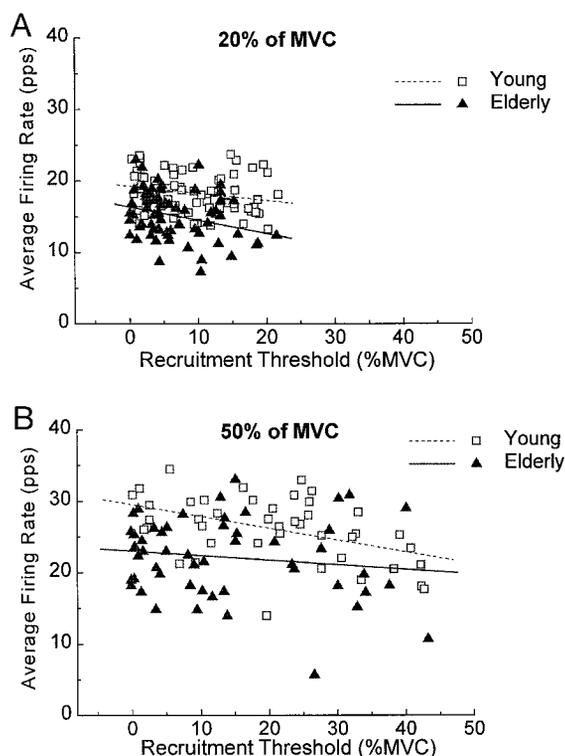
FIG. 5. Average firing rates of motor units vs. recruitment threshold in the young and the elderly at 20%-MVC (*A*) and 50%-MVC (*B*) force levels. The average firing rate was calculated by averaging the continuous mean firing rate signal in the 1st 5-s stable force region. The recruitment threshold is the averaged force in a window of 7.5 ms beginning at the time of the 1st firing of the motor unit. Linear least squares regression lines were fit to each data set from the young and the elderly.

$(-0.28 \pm 0.27 \text{ pps}^2$ for the young; $-0.16 \pm 0.24 \text{ pps}^2$ for the aged).

Average firing rates of motor units

The results from all the subjects in each group were pooled together for each force level. The average firing rate of each identified motor unit is plotted against its recruitment threshold in Fig. 5 for 20% (*A*) and for 50%-MVC (*B*) levels, with squares representing data from young subjects and triangles corresponding to aged subjects. Table 1 summarizes the parameters of the linear regression analyses at the two force levels. The firing rates of the motor units in the elderly were

TABLE 1. *Regression values on the average firing rates versus recruitment threshold relationships for the young and elderly at 20 and 50%-MVC force levels*

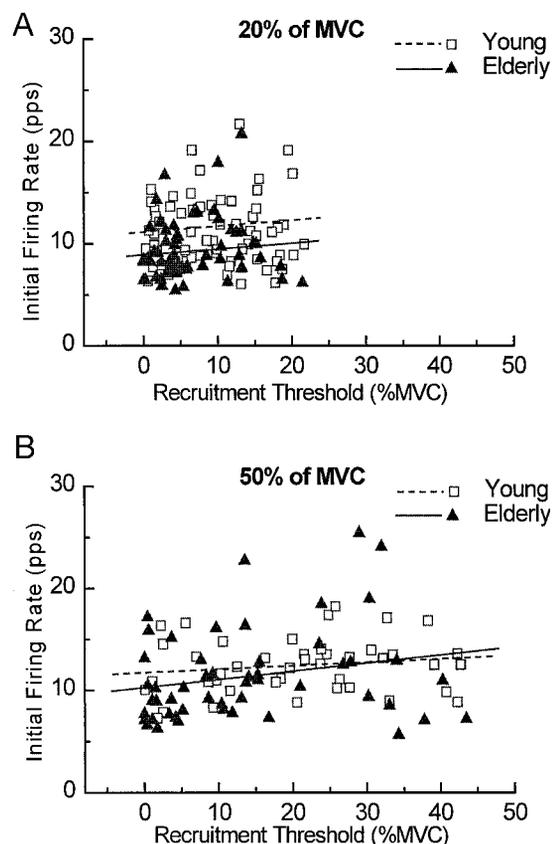|	Intercept	Slope	*R*	SD	*P*	*n*
			A. 20% of MVC			
Young	19.26	−0.09	−0.22	2.70	0.05	69
Elderly	16.37	−0.18	−0.28	3.19	0.01	68
			B. 50% of MVC			
Young	29.50	−0.16	−0.46	4.05	0.001	43
Elderly	22.99	−0.06	−0.14	5.56	0.31	51

MVC, maximal voluntary contraction.

FIG. 6. Initial firing rates vs. recruitment threshold at 20%-MVC (*A*) and 50%-MVC (*B*) force levels in the young and elderly. A linear least squares line was fit to each data set.

depressed in comparison to those observed in the young at both force levels as displayed by the regression lines fit to each group. The coefficients for the regression equations were compared at a significance level of 0.05 at each contraction level using the statistical tests described by Zar (1984). For the 20%-MVC case, the null hypothesis of equal regression line slopes for the young and the elderly was rejected, resulting in the rejection of the null hypothesis that the data from the young and elderly were generated by the same regression model. For the 50%-MVC case, the null hypothesis of equal slopes could not be rejected. The intercepts of these lines were then compared, and the null hypothesis of equal intercepts was rejected, thus resulting again in the rejection of the null hypothesis that the data from the young and elderly were generated by the same regression model. Averaging of the firing rates across motor units of all thresholds yielded 18.33 ± 2.76 pps for the young, 15.17 ± 3.31 pps for the aged at 20% MVC; and 26.08 ± 4.52 pps for the young, 22.11 ± 5.57 pps for the aged at 50% MVC. The difference between the age groups were significant ($P < 0.001$) for both force levels.

Initial firing rates

The initial firing rates of motor units in the elderly subjects were lower as compared with the young at both 20% and 50%-MVC force levels. Figure 6 shows the initial firing rate plotted as a function of the recruitment threshold for 20%-MVC (*A*) and 50%-MVC (*B*) contractions. As seen from the figure, the slight positive correlation between the initial firing

TABLE 2. *Regression values on the initial firing rates versus recruitment threshold relationship for the young and the elderly at 20 and 50%-MVC force levels*

	Intercept	Slope	R	SD	P	n
		A. 20% of MVC				
Young	11.48	0.05	0.07	4.89	0.5	69
Elderly	8.927	0.05	0.10	2.88	0.41	68
		B. 50% of MVC				
Young	11.73	0.03	0.15	2.69	0.30	43
Elderly	10.26	0.08	0.22	4.51	0.12	51

MVC, maximal voluntary contraction.

rates and recruitment threshold (Clamann 1970; De Luca and Erim 1994) is maintained in the elderly. Table 2 presents the parameters of the regression lines calculated for the two age groups at the two force levels. The regression equations were compared at a significance level of 0.05 at each contraction level using the same statistical tests employed for the comparison of average firing rate versus recruitment threshold comparisons. For both force levels, the null hypothesis of equal slopes for the two equations could not be rejected. The intercepts of these lines were then compared, and the null hypothesis of equal intercepts was rejected.

Coefficient of variation of interpulse intervals

In analyzing the variability among interpulse intervals, units recruited within 5%MVC of the target level were not considered. Such units, operating too close to their recruitment threshold, would be effectively turning on and off with slight fluctuations in drive, and hence were considered unstable. At 50% of MVC, the CV of interpulse intervals of a given motor unit was independent of the recruitment threshold of the unit in both age groups ($P > 0.10$), in agreement with our previous findings (Erim et al. 1995). Student's t-test revealed no statistically significant difference ($P > 0.05$) between coefficients of variation of the two groups at this force level (young: 0.283 ± 0.071; elderly: 0.301 ± 0.083). In contrast, at 20% of MVC, the CV of interpulse intervals appeared to be linearly related to recruitment threshold ($P < 0.005$) for the aged group, whereas it was independent of recruitment threshold for the young group ($P > 0.10$). A t-test between the two groups pointed to a statistically significant ($P < 0.005$) difference between the groups (young: 0.188 ± 0.078; elderly: 0.234 ± 0.074).

Distribution of recruitment thresholds

Recruitment was observed throughout the range up to 50% of MVC in both the young and the elderly. However, the recruitment threshold distribution in the elderly reflected a shift toward lower values. Figure 7 shows the percentage count of recruitment thresholds of motor units observed throughout the range in 20% (*A*) and 50%-MVC (*B*) trials. The recruitment thresholds were observed to be almost the same for motor units sampled from a single trial in many instances in the elderly. On the other hand, the recruitment thresholds of motor units sampled in a given trial were found to vary in a wider range in the young.
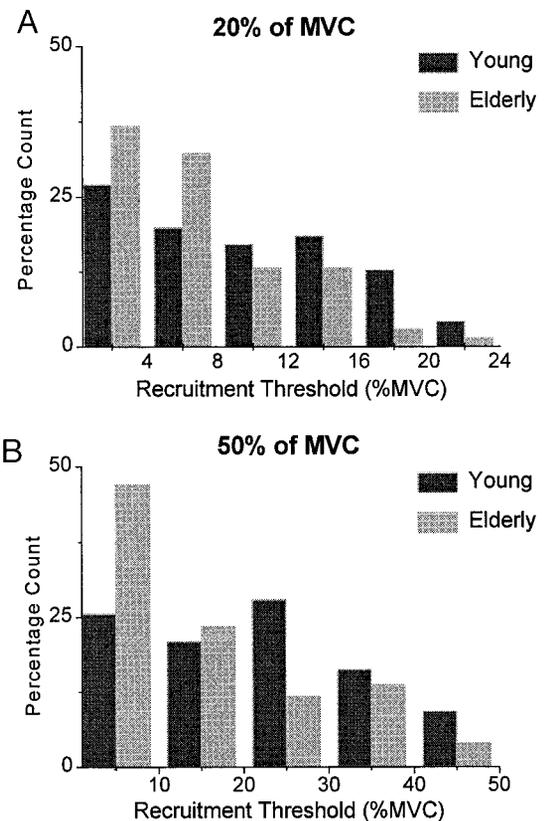

FIG. 7. Percentage distribution of recruitment thresholds at 20%-MVC (*A*) force level and 50%-MVC (*B*) force level. The percentage count was calculated by dividing the number of recruitment thresholds points observed in each bin by the total number of motor units on which the histogram was constructed. The total number of motor units in each group are 20% of MVC (*A*): 69 from young, 68 from elderly; 50% of MVC (*B*): 43 from young and 51 from elderly.

Maximal voluntary contraction force

The maximal voluntary contraction force measured at the beginning of each experiment was significantly different in the young and the aged subjects. The maximal force of abduction is plotted as a function of age in Fig. 8. A t-test between the groups indicated that the mean abduction forces in the two populations (37.5 ± 8.253 N in young and 27.4 ± 10.55 N in the elderly) were significantly different ($P < 0.05$). There was
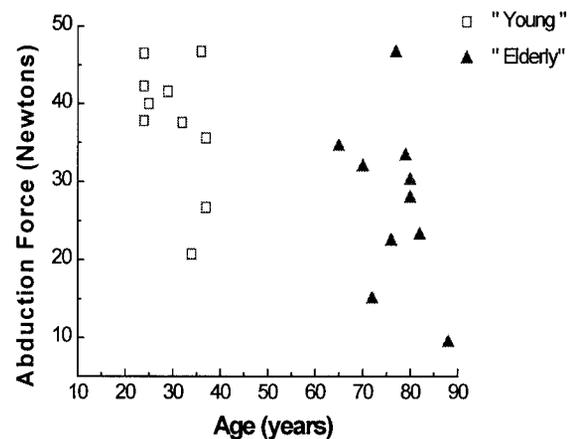

FIG. 8. Maximum abduction force of the 1st dorsal interosseous (FDI) plotted as a function of the subject's age.
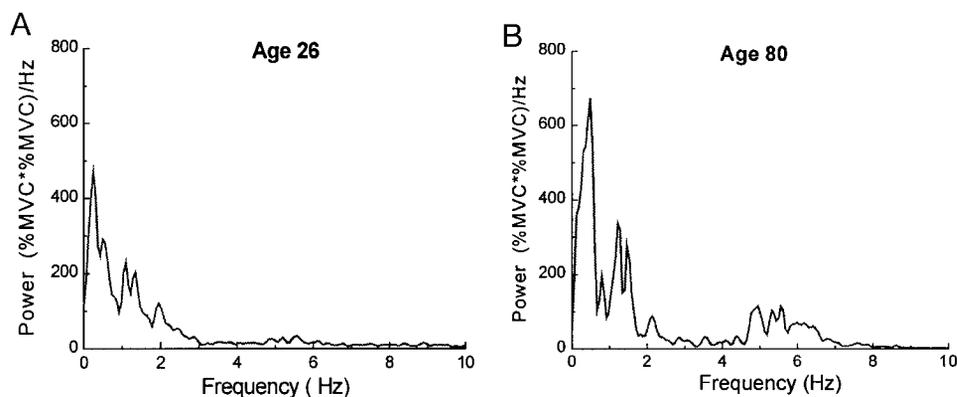
FIG. 9. Spectral content of the force recorded from a young and an elderly subject. In spite of high variability observed in the spectral content of both groups, on average, there was a trend toward higher frequencies in the force fluctuations in the elderly.

a high variation in the maximum strength among both the young and the elderly groups.

Fluctuations in force

The elderly subjects were able to track the presented trapezoidal trajectories with fair amount of accuracy in force. However, in many cases, the elderly subjects' force contained high-frequency fluctuations. The power spectral density estimate on the force plateau (60 s duration at 20% and 20 s duration at 50% of MVC) was calculated (Welch 1967) using 10-s duration windows with 50% overlap to examine whether the spectral content differed in some fashion from the young. Even though there was variability in each group, power was in general distributed over a greater bandwidth in the elderly as exemplified in Fig. 9.

The CV of force (defined as the ratio of the standard deviation to the mean of the force signal) was calculated over the entire force plateau at both 20%-MVC level (young: 0.031 ± 0.012; elderly: 0.030 ± 0.010) and 50%-MVC level (young: 0.028 ± 0.005; elderly: 0.030 ± 0.013). A *t*-test on the CV of force between the young and the elderly groups indicated that it was not significantly different (using significance level $P < 0.05$) at either force level.

Satellite potentials and polyphasic potentials

Satellite and polyphasic motor-unit action potentials (MUAPs) were observed in the signals recorded from the elderly muscle. Figure 10 shows MUAPs recorded via the intramuscular needle electrode from two elderly subjects. In Fig. 10*A* a distinct satellite potential fires after the first potential, and in *B,* two satellite potentials fire after the first potential. Satellite potentials suggest reinnervation of a group of

orphaned fibers by collateral nerve sprouting from a surviving axon (Dorfman et al. 1988). Motor units possessing these satellite potentials were detected more often in the elderly (in all, 8 satellite potentials from 4 elderly subjects were observed as compared with 2 satellite potentials from 1 young subject).

DISCUSSION

The most important contribution of this work has been to offer insight into the age-related changes in the time course of motor-unit firing patterns throughout a contraction. In addition to the decrease in average firing rates, which had been reported before, our results reveal that there are significant modifications in the instantaneous behavior of aged motor units, which are averaged out when average firing rates over the whole contraction are used. For example, when only average firing rates are considered, it would seem that the main effect of aging is similar to that of hand dominance: a decrease in the firing rates (Adam et al. 1998) that could be explained by the general slowing of the muscle with a shift toward type I fibers. However, the investigation of the firing rates as a function of time throughout the contraction along with the interaction between the firing rates of concurrently active motor units reveal significant differences between the two paradigms and suggest important age-induced alterations in the control of motor units.

Time-varying behavior of motor units

DECREASE IN COMMON DRIVE. The most striking finding of this study is the decrease in the commonality of motor-unit firings in the elderly. This diminished commonality, manifest in the decreased correlation among the fluctuations in motor-unit firing rate as well as the different firing rate trends raises the
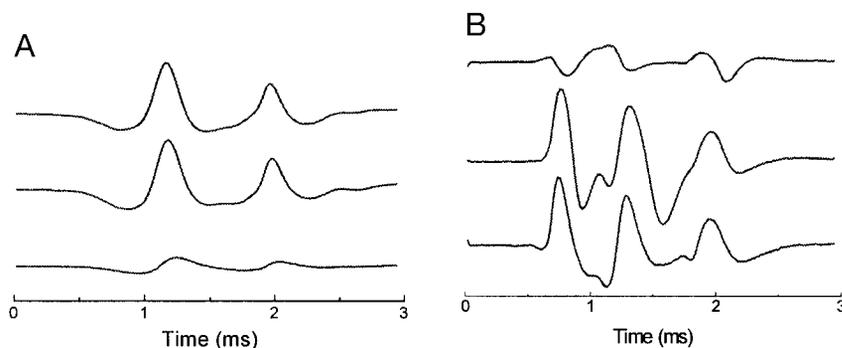

FIG. 10. Satellite potentials in the intramuscular signals acquired from 2 elderly subjects via the quadrifilar electrode. Three views of the same motor-unit action potential (MUAP) provided by the 3 channels of the electrode are plotted with the associated time scale. Satellite potentials indicate collateral reinnervation of orphaned fibers by surviving motor units.

question as to whether the natural aging process results in significant modifications to the arrangement of the motoneuron pool.

The most direct explanation for the observed decrease in the correlation among the firing activities of concurrently active motor units would be a decrease in the ratio of shared versus unshared inputs received by the motor units. This decrease could come about via a decrease in the common inputs, an increase in the unshared inputs, or a combination thereof. The balance of shared versus unshared inputs to motor units can be altered by age-related changes in spindles including increased capsular thickness, a decrease in the mean number of intrafusal fibers per spindle, spherical axonal swellings and degenerative changes in the spindle neuromuscular end plates (Swash and Fox 1972), and a decrease in reflex sensitivity resulting from a decline in the spindle sensitivity with age (Corden and Lippold 1996); by the atrophy and reinnervation that modifies the afferent input from Golgi tendon organs that are sensitive to contractions of single motor units (Binder et al. 1977); age-related changes in presynaptic inhibition of Ia afferent terminals (Butchart et al. 1993); decrease in Ia facilitation (Morita et al. 1995); a change in distribution of synaptic strength among individual motoneurons within the pool, caused by sprouting of motoneuron dendrites and Ia fibers and formation of new synapses between them (Ramirez and Ulfhake 1992); increased synaptic noise (Poliakov et al. 1996); and possible neurodegenerative processes in the corticospinal tract (Lexell 1997). Although in other muscles the Renshaw cells that receive more excitation from the larger α-motoneurons (Hultborn et al. 1988) may also play a role in disturbing the shared/unshared input ratio, in the FDI Renshaw inhibition is most likely absent as in the distal muscles controlling the digits (Rossi and Mazzachio 1991), in particular the opponens policis and the abductor digiti minimi in the upper limb (Katz et al. 1993).

CROSS-OVER: VIOLATION OF THE ONION SKIN PHENOMENON. The disturbance to the onion skin phenomenon and the observation of cross-over as well as different mean firing rate trends among the motor units of the elderly may be a direct result of a decrease in common drive. If motor units are responding to significantly different drives, they cannot be expected to keep the orderly relationship among their firing rates. However, the possibility of a disturbance in the intrinsic excitability and firing responses of motoneurons cannot be ruled out. A decreased sensitivity to excitation has been reported for aged motoneurons (McComas 1977). Apparently at odds with this report, but nonetheless demonstrating a disturbance in the excitation/firing rate characteristics, Morales et al. reported that motoneuron rheobase current was lower in aged compared with young adult cats (Morales et al. 1987).

Another possible contributor to the cross-over phenomenon in the elderly is the disturbance to the tight relationship between the electrical and mechanical properties of the motor unit due to the collateral reinnervation process (Ansved and Larsson 1990, 1995; Campbell et al. 1973; Doherty et al. 1993a,b; Kadhiresan et al. 1996; Kanda and Hashizume 1989; Lexell et al. 1988). It has been reported that in the FDI, the correlation between the macro EMG (which is a measure of the size of the motor unit) and the recruitment threshold (a measure of the size of the motoneuron) is decreased with age (Masakado et al. 1994). In another study, it was concluded that

due to reinnervation of fibers with age, the higher conduction velocity fibers may be innervated by the smaller motoneurons and thus may be recruited earlier in older subjects (Merletti et al. 1992). This age-induced decoupling among various properties of the motor unit may result in a "loosening" of the relationship between the recruitment order and firing rate of the motor unit. Even if the recruitment threshold of the neuron (an inherent membrane property) may remain unaltered, the firing behavior of the neuron, once it is recruited, may be affected by the actual force output and/or the fatiguability properties of the muscle fibers it innervates through some yet unclear feedback mechanism. Hence a mismatch in the type of the neuron and the type of orphan fibers it picks up can cause a disturbance in the recruitment threshold/firing rate relationship.

LACK OF DECREASE IN FIRING RATES DURING SUSTAINED CONTRACTIONS. In the elderly, the systematic decrease in firing rates of motor units during a sustained contraction was not observed consistently. In many cases, concurrently active motor units displayed differing trends in their firing rates, with some motor units increasing their firing rates while others decreased or maintained their firing rates. The mechanisms previously proposed to account for the progressive decrease in the firing rates include a combination of the late adaptation properties of the motoneuron (Kernell 1965; Kernell and Monster 1982) and an accompanying decrease in drive to the motoneuron pool (De Luca et al. 1996) due to twitch potentiation of motor units (Macintosh et al. 1994; Vandervoort et al. 1983). Aging has been shown to be associated with decreased twitch potentiation in the tibialis anterior muscle of humans (Hicks et al. 1991) and the medial gastrocnemius of rats (Kanda and Hashizume 1989). If the twitch potentiation capacity is decreased also in the FDI due to the aging process, it would be in line with the observed absence of firing rate decline. Another reason for the lack of decrease in firing rates may be the selective loss of larger motor units, as reflected in the significant difference observed in firing rate drops at 50% MVC and lack thereof at 20% MVC. At the low level, both age groups use low-threshold motor units that show the least potentiation (Burke 1981) that leads to minimal firing rate slopes (De Luca et al. 1996) in both age groups. However, at the 50%MVC level where all motor units are expected to be recruited in the FDI (De Luca et al. 1982a,b; Milner-Brown et al. 1973), the elderly are still limited to the small, low-threshold units, whereas the young rely on high-threshold motor units that display the most potentiation (Burke 1981) and hence the greatest firing rate decrease.

Time-averaged motor-unit parameters

In addition to the novel findings regarding the time course of firing rates during constant-force contractions, our study yielded several findings that had been reported by other groups (for a review of age-related changes in motor unit function, see Roos et al. 1997).

DECREASED AVERAGE FIRING RATES. Several studies (Howard et al. 1988; Nelson et al. 1984; Newton et al. 1988; Soderberg et al. 1991) have reported a general decrease in firing rates in older subjects, in agreement with our findings displayed in Fig. 5. In contrast to these reports, no age-related change was observed in the firing behavior of motor units in the FDI during

a "threshold" task (where the force level was just sufficient to maintain a constant, low discharge rate for a single motor unit value) by Galganski and coworkers (Galganski et al. 1993). Others reported no change at 50%MVC (Kamen et al. 1995) and decreased firing rates at higher (Roos and Rice 1996) or maximal force levels (Kamen et al. 1995). These different results may have arisen from the difference in the controlled parameter (firing rate as opposed to force output), or differences in calculating the average firing rate, neglecting the dependency of firing rates on recruitment threshold and considering an overall average firing rate for the whole motor-unit population (thereby allowing motor units with different thresholds to weigh differently in the average).

Some of the possible mechanisms underlying the decrease in firing rates are a decrease in excitability of axonal membranes with age (McComas 1977) and a decrease in the net drive to the motoneuron pool (Kamen et al. 1995) resulting in a decrease in firing rates. The increase in the size of surviving motor units due to reinnervation (Ansved and Larsson 1995; Kanda and Hashizume 1989) leading to increased twitch forces, the increase in the contraction times and half-relaxation times of the surviving motor units (Campbell et al. 1973; Doherty and Brown 1993; Kanda and Hashizume 1989; Newton et al. 1988; Newton and Yemm 1986), the increase in the percentage of type I fibers, and the decrease in the percentage of type II (Ansved and Larsson 1995; Grimby et al. 1982; Larsson 1995; Larsson et al. 1977) are all factors that require lower firing rates. Slower twitch characteristics would require lower firing rates to fuse. Likewise, the increased amplitude of motor-unit twitches, combined with the availability of a larger number of lower threshold, type I motor units at a given force level enable the muscle to produce the required force with lower firing rates.

The suggestion that the slowing of the muscle results in lower firing rates may seem at odds with the onion skin phenomenon. It may appear that because according to the onion skin notion, slower-twitch motor units maintain higher firing rates, a shift in the fiber composition toward slower-twitch units would result in higher firing rates. However, onion skin is a result of the need to match, within a given pool, the firing rates to the fatiguability of the motor units and not to achieve maximum fusing of twitches (De Luca et al. 1982a; De Luca and Erim 1994). On the other hand, given a set of motor units, a general slowing of the fibers would decrease the need for high firing rates, because in this case the twitches fuse at lower firing rates. However, also among the units of the "slowed-down" muscle, the relationship of onion skin would be expected to hold if a systematic slowing of the muscle were the only alteration in question. For instance, in the case of hand-dominance where an increase in type I fibers reflects slower fiber characteristics and consequent lower firing rates, the onion skin relationship is nonetheless maintained in the dominant and nondominant sides (Adam et al. 1998). The violation of the onion skin phenomenon in the elderly is an indication that there exist significant alterations to the motoneuron pool organization in addition to the slowing down of the muscle.

Our finding of an age-related shift toward lower recruitment thresholds is at odds with a previous report of a shift toward higher levels (Galganski et al. 1993). In that study, the subjects were instructed to maintain the discharge of a single motor unit at a constant low rate. This resulted in the elderly subjects contracting ~50% more than their young counterparts in terms of MVC. Hence, were the two groups to activate their muscles at the same level, it is likely that the young subjects would recruit many more of their higher recruitment threshold motor units, revealing a different recruitment threshold distribution.

Force output

As expected from the obvious signs of muscle atrophy and waste, the mean MVC force for the young and the elderly subject groups were found to be significantly different ($P < 0.05$) using the t-test. However, the CV of force throughout the contraction revealed no statistically significant difference among the two age groups at either force level. In contrast, Galganski and coworkers (Galganski et al. 1993) found a higher CV of force in the elderly. In a similar study, Keen et al. found higher CV of force at levels up to 20% MVC, but no significant difference at 50%MVC (Keen et al. 1994). Galganski et al. (1993) found no difference between the two age groups in terms of the CV of interpulse intervals. In the present study, although there was no significant difference at 50%MVC, the CV of interpulse intervals was higher in the elderly at 20% MVC. Although these conflicting results do not draw a clear picture, our finding of increased CV of interpulse intervals at 20% MVC, considered in light of the increased CV observed by Keen et al., may indicate a mechanism for compromised motor control at lower force levels in the elderly.

This study has revealed that significant changes in the control properties accompany age-related alterations in the morphology of motor units. Some of these changes, like the reduction in the average firing rates in response to a general slowing of muscle fibers, can be speculated to be a direct result of the changes in mechanical properties. However, it remains to be understood if other age-related changes, specifically the decrease in the common drive and onion skin behavior observed in this study, are compensatory/adaptive mechanisms to mitigate the diminutive effects of aging on the musculature as suggested by Roos et al. (Roos et al. 1997); or if they are independent, age-induced insults to the neural control of muscles that might be stopped or reversed through appropriate training and neural "relearning."

REFERENCES

ADAM, A., DE LUCA, C., AND ERIM, Z. Hand dominance and motor unit firing behavior. *J. Neurophysiol.* 80: 1373–1382, 1998.

ANSVED, T. AND LARSSON, L. Quantitative and qualitative morphological properties of the soleus motor nerve and the L5 ventral root in young and old rats. *J. Neurol. Sci.* 96: 269–282, 1990.

ANSVED, T. AND LARSSON, L. Effects of aging on the motor unit. *Prog. Neurobiol.* 45: 397–458, 1995.

BINDER, M. D., KROIN, J. S., MOORE, G. P., AND STUART, D. G. The response of Golgi tendon organs to single motor unit contractions. *J. Physiol. (Lond.)* 271: 337–349, 1977.

BURKE, R. E. Motor units. Anatomy, physiology, and functional organization. In: *Handbook of Physiology. The Nervous System. Motor Control.* Bethesda, MD: Am. Physiol. Soc., 1981, sect. 1, vol. II, p. 345–422.

BUTCHART, P., FARQUHAR, R., PART, N., AND ROBERTS, R. The effect of age and voluntary contraction on presynaptic inhibition of soleus muscle Ia afferent terminals in man. *Exp. Physiol.* 78: 235–242, 1993.

CAMPBELL, M. J., McCOMAS, A. J., AND PETITO, F. Physiological changes in ageing muscle. *J. Neurol. Neurosurg. Psychiatry* 36: 174–182, 1973.

CLAMANN, H. P. Activity of single motor units during isometric tension. *Neurology* 20: 254–260, 1970.

CORDEN, D. M. AND LIPPOLD, O. C. J. Age-related impaired reflex sensitivity in a human hand muscle. *J. Neurophysiol.* 76: 2701–2705, 1996.

DE LUCA, C. J. Precision decomposition of EMG signals. *Methods Clin. Neurophysiol.* 4: 1–28, 1993.

DE LUCA, C. J. AND ERIM, Z. Common drive of motor units in regulation of muscle force. *Trends Neurosci.* 17: 299–305, 1994.

DE LUCA, C. J., FOLEY, P. J., AND ERIM, Z. Control properties of motor units in constant-force isometric contractions. *J. Neurophysiol.* 76: 1503–1516, 1996.

DE LUCA, C. J., LEFEVER, R. S., McCUE, M. P., AND XENAKIS, A. P. Behaviour of human motor units in different muscles during linearly varying contractions. *J. Physiol. (Lond.)* 329: 113–128, 1982a.

DE LUCA, C. J., LEFEVER, R. S., McCUE, M. P., AND XENAKIS, A. P. Control scheme governing concurrently active human motor units during voluntary contractions. *J. Physiol. (Lond.)* 329: 129–142, 1982b.

DOHERTY, T. J. AND BROWN, W. F. The estimated numbers and relative sizes of thenar motor units as selected by multiple point stimulation in young and older adults. *Muscle Nerve* 16: 355–366, 1993.

DOHERTY, T. J., VANDERVOORT, A. A., AND BROWN, W. F. Effects of ageing on the motor unit: a brief review. *Can. J. Physiol.* 18: 331–358, 1993a.

DOHERTY, T. J., VANDERVOORT, A. A., TAYLOR, A. W., AND BROWN, W. F. Effects of motor unit losses on strength in older men and women. *J. Appl. Physiol.* 74: 868–874, 1993b.

DORFMAN, L. J., HOWARD, J. E., AND McGILL, K. C. Influence of Contractile forces on properties of motor unit action potentials: ADEMG analysis. *J. Neurol. Sci.* 86: 125–136, 1988.

ERIM, Z. *Evaluation of Common Drive of Motor Unit Discharges* (PhD dissertation). Boston, MA: Boston University, 1992.

ERIM, Z., DE LUCA, C., AND MINEO, K. Control of motor units in the generation of muscle force. In: *XVth Congress of the International Society of Biomechanics in University of Jyvaskyla, Finland*, edited by K Hakkinen, K. L. Keskinen, P. V. Komi, and A. Mero. Finland: Gummerus Printing, 1995, p. 254–255.

ERIM, Z., DE LUCA, C., MINEO, K., AND AOKI, T. Rank-ordered regulation of motor units. *Muscle Nerve* 19: 563–573, 1996.

GALGANSKI, M. E., FUGLEVAND, A. J., AND ENOKA, R. M. Reduced control of motor output in a human hand muscle of elderly subjects during submaximal contractions. *J. Neurophysiol.* 69: 2108–2115, 1993.

GRIMBY, G., DANNESKIOLD-SAMSOE, B., HVID, K., AND SALTIN, B. Morphology and enzymatic capacity in arm and leg muscles in 78–81 year old men and women. *Acta Physiol. Scand.* 115: 125–134, 1982.

HICKS, A., CUPIDO, C., MARTIN, J., AND DENT, J. Twitch potentiation during fatiguing exercise in the elderly: the effects of training. *Eur. J. Appl. Physiol.* 63: 278–281, 1991.

HOWARD, J. E., McGILL, K. C., AND DORFMAN, L. J. Age effects on properties of motor unit action potentials: ADEMG analysis. *Ann. Neurol.* 24: 207–213, 1988.

HULTBORN, H., LIPSKI, J., MACKEL, R., AND WIGSTROM, H. Distribution or recurrent inhibition within a motor nucleus. I. Contribution from slow and fast motor units to the excitation of Renshaw cells. *Acta Physiol. Scand.* 134: 347–361, 1988.

KADHIRESAN, V. A., HASSETT, C. A., AND FAULKNER, J. A. Properties of single motor units in medial gastrocnemius muscles of adult and old rats. *J. Physiol. (Lond.)* 493: 543–552, 1996.

KAMEN, G. AND DE LUCA, C. Motor unit firing behavior in the aged. In: *Computer-Aided Electromyography and Expert Systems*, edited by J. E. Desmedt. New York: Elsevier Science Publishers B.V., 1989, p. 231–239.

KAMEN, G., SISON, S. V., DU, C.C.D., AND PATTEN, C. Motor unit discharge behavior in older adults during maximal effort contractions. *J. Appl. Physiol.* 79: 1908–1913, 1995.

KANDA, K. AND HASHIZUME, K. Changes in properties of the medial gastrocnemius motor units in aging rats. *J. Neurophysiol.* 61: 737–746, 1989.

KATZ, R., MAZZOCHIO, R., PENICAUD, A., AND ROSSI, A. Distribution of recurrent inhibition in the human upper limb. *Acta Physiol. Scand.* 149: 183–198, 1993.

KEEN, D., YUE, G., AND ENOKA, R. Training related enhancement in the control of motor output in elderly humans. *Physiol. J. Appl.* 77: 2648–2658, 1994.

KERNELL, D. The adaptation and the relation between discharge frequency and current strength of cat lumbosacral motoneurones stimulated by long-lasting injected currents. *Acta Physiol. Scand.* 65: 65–73, 1965.

KERNELL, D. AND MONSTER, A. W. Time course and properties of late adaptation in spinal motoneurones of the cat. *Exp. Brain Res.* 46: 191–196, 1982.

LARSSON, L. Motor units: remodeling in aged animals. *J. Gerontol. Biol. Sci. Med. Sci.* 50: 91–95, 1995.

LARSSON, L., SJODIN, B., AND KARLSSON, J. Histochemical and biochemical changes in human skeletal muscle with age in sedentary males, age 22–65 years. *Acta Physiol. Scand.* 103: 31–39, 1977.

LEFEVER, R. S. AND DE LUCA, C. J. A procedure for decomposing the myoelectric signal into its constituent action potentials. Part I. Technique, theory and implementation. *IEEE Trans. Biomed. Eng.* 29: 149–157, 1982.

LEFEVER, R. S., XENAKIS, A. P., AND DE LUCA, C. J. A procedure for decomposing the myoelectric signal into its constituent action potentials. Part II. Execution and test for accuracy. *IEEE Trans. Biomed. Eng.* 29: 158–164, 1982.

LEXELL, J. Evidence for nervous system degeneration with advancing age. *J. Nutr.* 127: 1011S–1013S, 1997.

LEXELL, J., SJOSTROM, M., AND TAYLOR, C. C. What is the cause of ageing atrophy? Total number, size and proportion of different fiber types studied in whole vastus lateralis muscle from 15–83-year-old men. *J. Neurol. Sci.* 84: 275–294, 1988.

MACINTOSH, B. R., GRANGE, R. W., CORY, C. R., AND HOUSTON, M. E. Contractile properties of rat gastrocnemius muscle during staircase fatigue and recovery. *Exp. Physiol.* 79: 59–70, 1994.

MAMBRITO, B. AND DE LUCA, C. J. A technique for the detection, decompositon and analysis of the EMG signal. *Electroencephalogr. Clin. Neurophysiol.* 59: 175–188, 1984.

MASAKADO, Y., NODA, Y., NAGATA, M., KIMURA, A., CHINO, N., AND AKABOSHI, K. Macro-EMG and motor unit recruitment threshold: differences between the young and the aged. *Neurosci. Lett.* 179: 1–4, 1994.

McCOMAS, A. J. Ageing. In: *NeuroMuscular Function and Disorders*. New York: Butterworths, 1977, p. 101–108.

MERLETTI, R., LO CONTE, L. R., ACTIS, M. V., AND CISARI, C. Age related changes in surface myoelectric signals. *Scand. J. Rehab. Med.* 24: 25–36, 1992.

MILNER-BROWN, H. S., STEIN, R. B., AND YEMM, R. The contractile properties of human motor units during voluntary isometric contractions. *J. Physiol. (Lond.)* 228: 285–306, 1973.

MORALES, F., BOXER, P., FUNG, S., AND CHASE, M. Basic electrophysiological properties of spinal cord motoneurons during old age in cats. *J. Neurophysiol.* 58: 180–194, 1987.

MORITA, H., SHINDO, M., YANAGAWA, S., YOSHIDA, T., MOMOI, H., AND YANAGISAWA, N. Progressive decrease in heteronymous monosynaptic Ia facilitation with human ageing. *Exp. Brain Res.* 104: 167–170, 1995.

NELSON, R. M., SODERBERG, G. L., AND URBSCHEIT, N. L. Alteration of motor-unit discharge characteristics in aged humans. *Phys. Ther.* 64: 29–34, 1984.

NEWTON, J. P. AND YEMM, R. Changes in contractile properties of the human first dorsal interosseus muscle with age. *Gerontology* 32: 98–104, 1986.

NEWTON, J. P., YEMM, R., AND McDONAGH, M.J.N. Study of age changes in the motor units of the first dorsal interosseous muscle in man. *Gerontology* 34: 115–119, 1988.

PERSON, R. S. AND KUDINA, L. P. Discharge frequency and discharge Pattern of human motor units during voluntary contraction of muscle. *Electroencephalogr. Clin. Neurophysiol.* 32: 471–483, 1972.

POLIAKOV, A., POWERS, R., SAWCZUK, A., AND BINDER, M. Effects of background noise on the response of rat and cat motoneurones to excitatory current transients. *J. Physiol. (Lond.)* 495: 143–157, 1996.

RAMIREZ, V. AND ULFHAKE, B. Anatomy of dendrites in motoneurons in supplying the intrinsic muscles of the foot sole in the aged cat: evidence for dendritic growth and neo-synaptogenesis. *J. Comp. Neurol.* 316: 1–16, 1992.

Roos, M. R. and Rice, C. L. Age-related changes in neuromuscular properties of human quadriceps. *Med. Sci. Sports Exerc.* 28: S163, 1996.

Roos, M. R., Rice, C. L., and Vandervoort, A. A. Age-related changes in motor unit function. *Muscle Nerve* 20: 679–690, 1997.

Rossi, A. and Mazzachio, R. Presence of homonymous recurrent inhibition in motoneurons in supplying different lower limb muscles in humans. *Exp. Brain Res.* 84: 367–373, 1991.

Soderberg, G. L., Minor, S. D., and Nelson, R. M. A comparison of motor unit behaviour in young and aged subjects. *Age Ageing* 20: 8–15, 1991.

Swash, M. and Fox, K. P. The effect of age on human skeletal muscle: studies of the morphology and innervation of muscle spindles. *J. Neurol. Sci.* 16: 417–432, 1972.

Vandervoort, A. A., Quinlan, J., and McComas, A. J. Twitch potentiation after voluntary contraction. *Exp. Neurol.* 81: 141–152, 1983.

Welch, P. The use of fast Fourier transform for the estimation of power spectra: a method based on time averaging over short, modified periodograms. *IEEE Trans. Audio ElectroAcoust.* AU-15: 70–73, 1967.

Zar, J. H. Comparing simple linear regression equations. In: *Biostatistical Analysis.* Englewood Cliffs, NJ: Prentice-Hall, 1984, p. 292–305.