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Age-Related Muscle Fatigue After a Low-Force Fatiguing Contraction is Explained by Central Fatigue

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Abstract

The contribution of central fatigue during and after low- and high-force isometric contractions sustained until failure with age is not established. We compared the time to failure and changes in voluntary activation

measured using motor point stimulation of 15 young and 15 old adults for an isometric contraction sustained with the elbow flexor muscles at 20% and 80% of maximal voluntary contraction (MVC) force. Young adults had a briefer time to task failure than old adults for the 20% MVC fatiguing contraction, but a similar duration for the 80% task. Voluntary activation was reduced at the end of the 20% MVC task, but by greater magnitudes for old than young adults. The reduction in MVC torque after the low-force task was associated with the reduction in voluntary activation. After the 80% task, voluntary activation declined to similar levels for the young and old adults. Electromyographic activity levels (% MVC) of the biceps brachii and brachioradialis muscles during the fatiguing contraction were greater for the old than young for the 20% MVC task, but similar with age for the 80% MVC task. Our findings indicate that intensity and duration of contraction can be manipulated in young and old adults to induce varying magnitudes of fatigue within the central nervous system. Aging increases: (1) fatigue within the central nervous system immediately after a low-force fatiguing contraction, and (2) the potential for large neural adaptations during neuromuscular rehabilitation in old adults.

Age-related changes within the central nervous system may predispose old adults to impairment of the neuromuscular system. Some of these changes include age-related structural degradation of the cortical neuron⁸ and smaller cortical size,⁴¹ reduced excitability of the motor cortex and motoneuron pool,^{40,43} a decline in effective connectivity between motor-related cortical areas,⁴² and motoneuron degeneration.³⁶ These changes may ultimately impair neural drive to the muscle and force production during voluntary contractions.

Voluntary activation is quantified in young and old adults as the extra force elicited by stimulating the motor nerve during a maximal voluntary contraction (MVC).¹³ This extra evoked force indicates that either the motor units were not all recruited voluntarily or they were discharging at rates that were not high enough to produce full fusion of force.¹⁸ Voluntary activation may be reduced with aging during brief maximal efforts when the muscle is not fatigued,^{5,46,50} but this is not the case for all muscle groups.²⁸ For healthy old adults who show initial decrements in voluntary activation, practicing maximal contractions may increase voluntary activation to levels similar to those of young adults.^{4,22,25}

Exercise-induced impairment of voluntary activation, or central fatigue,¹³ contributes significantly to impairment of force during and after long-duration, low-force contractions in young adults and varies with contraction intensity.^{44,49} It is not clear, however, whether old adults have greater exercise-induced impairment of voluntary activation than young adults because the literature is conflicting. Dorsiflexor muscles and a submaximal intermittent protocol with the elbow flexor muscles showed no age differences in central fatigue.^{2,4,34} Several muscle groups, however, exhibit age-related central fatigue including the knee extensor muscles and sustained contractions with the elbow flexor muscles.^{5,6,22,46} The magnitude of age-related central fatigue appears to be influenced by the type of contraction during which voluntary activation is assessed. For example, Bilodeau et al.⁶ found that force was evoked in the elbow flexor muscles of old adults with an electrical stimulus at the end of a moderate-intensity (35% MVC) isometric contraction sustained until failure, but not in young adults. In contrast, there was no age difference in voluntary activation when assessed during maximal effort immediately after the fatiguing contraction.⁶ We aimed to re-evaluate reductions in voluntary activation by stimulating the motor nerve during maximal effort during and after a fatiguing contraction in old adults. We assessed varying intensities of fatiguing contractions in the same cohort of young and old adults to understand the contribution of central fatigue with age during and after a low- and high-force task sustained until failure. We hypothesized that the decline in voluntary activation for old adults would be greater than for young adults after the low-force fatiguing contraction, but not after the high-force fatiguing contraction sustained until failure.

METHODS

Fifteen young adults (6 men and 9 women; mean \pm SD: 21.9 \pm 3.6 years of age) and 15 old adults (6 men and 9 women; 70.1 \pm 4.3 years) were recruited for this study. Because the sex of the individual influences the time to failure of a contraction,^{21,24} the proportion of young men ($n = 6$) and women ($n = 9$) recruited matched that of the old men and women. All subjects were healthy with no known neurological or cardiovascular diseases and were naive to the protocol. Prior to participation, each subject provided informed consent, and the protocol was approved by our institutional review board.

Subjects reported to the laboratory on three occasions, once for a familiarization session and twice for experimental sessions that were 7–10 days apart, to perform a protocol that focused on a fatiguing contraction with the elbow flexor muscles of the non-dominant arm. The introductory session involved a physical activity questionnaire, familiarization of each subject to the electrical-stimulation procedures, and the practice of brief submaximal contractions and MVCs. The physical activity level for each subject was assessed with a questionnaire that estimated the relative kilocalorie expenditure of energy per week.³¹ All subjects were right-handed (0.71 \pm 0.2 vs. 0.77 \pm 0.2 for young and old adults, respectively, with a ratio of 1 indicating complete right-handedness) as estimated using the Edinburgh Handedness Inventory.³⁹ The experimental sessions involved maintaining an isometric fatiguing contraction equivalent to 20% or 80% of MVC force for as long as possible. The order of the experimental sessions was randomized among subjects.

Mechanical Recording.

Subjects were seated upright in an adjustable chair with the non-dominant arm abducted slightly and the elbow resting on a padded support. The elbow joint was flexed to 90° so that the forearm was horizontal to the ground and the force at the wrist was directed upward when the elbow flexor muscles were activated during a voluntary contraction. Two nylon straps were placed vertically over each shoulder to restrain the subject and minimize shoulder movement. The hand and forearm were placed in a modified wrist–hand–thumb orthosis (Orthomerica, Newport Beach, California) and the forearm was placed midway between pronation and supination. The orthosis was attached to a force transducer (Force-Moment Sensor; JR-3, Inc., Woodland, California) mounted on a custom-designed, adjustable support to measure forces exerted by the wrist in the vertical direction. The forces detected by the transducer were recorded online using a Power 1401 A-D converter and Spike2 software (Cambridge Electronic Design, Cambridge, UK) and displayed on a 19-inch monitor located at eye level and 1.5 m in front of the subject. The force was adjusted for each subject during the submaximal tasks so a horizontal cursor that represented the required target force was displayed at ~60% the height of the screen. Each subject was asked to trace the horizontal cursor with the force signal as it appeared on the screen from the right side of the monitor at 2.5 cm/s.

Electrical Recordings.

Electromyographic (EMG) signals were recorded with bipolar surface electrodes (Ag/AgCl, 8-mm diameter, 16 mm between electrodes) that were placed over biceps brachii, brachioradialis, and triceps brachii muscles. Reference electrodes were placed on a bony prominence at the elbow. The EMG signal was amplified (100 \times) and band-pass filtered (13–1000 Hz) with Coulbourn modules (Coulbourn Instruments, Allentown, Pennsylvania) prior to being recorded directly to a computer using the Power 1401 A-D converter and Spike2 software (CED, Cambridge, UK). The EMG signals were digitized at 2000 samples/s.

Electrical Stimulations.

Electrical stimulation of the muscle was used to evoke force in the biceps brachii muscle to assess voluntary activation during each MVC performed throughout the protocol. The stimulating cathode was placed over the biceps brachii (midway between the anterior edge of the deltoid and antecubital fossa) and an anode was

placed over the bicipital tendon (2 cm proximal to the elbow).^{1,48} Activation of the muscle was achieved by a constant-current stimulator (DS7AH; Digitimer, Ltd., Welwyn Garden City, UK) that delivered a rectangular pulse of 100- μ s duration at an amplitude of 400 V. Twitch contractions were evoked at a supramaximal level of stimulation (\sim 200 mA to 500 mA). Supramaximal stimulation was determined by increasing the current for each twitch until the twitch force plateaued and was within 5% of the previous twitch amplitude. Once this intensity was achieved, the current was further increased by 10%. This level of stimulation was used for the remainder of the protocol. Twitches were evoked during MVCs performed before, during, and after the fatiguing contractions and at rest after each MVC when the muscle was potentiated (control twitch).¹³

Experimental Protocol.

The protocol for each experimental session comprised the following procedures: (1) determination of supramaximal levels of electric stimulation; (2) assessment of the MVC and voluntary activation for the elbow flexor muscles; (3) performance of MVCs of the elbow extensor muscles; (4) brief submaximal isometric contractions of the elbow flexor muscles at varying intensities to determine the force–EMG and force–voluntary activation relations; and (5) performance of a fatiguing contraction at either 20% or 80% of MVC force, immediately followed by a twitch contraction, a recovery MVC with the elbow flexor muscles, and another twitch contraction to determine voluntary activation.

MVC and Voluntary Activation.

Before the fatiguing contraction, each subject performed four MVC trials with the elbow flexors, followed by MVC trials with the elbow extensor muscles. MVCs with the elbow extensor muscles were performed so that maximal EMG could be recorded and used to normalize the triceps EMG activity during the fatiguing contractions. The MVC task for each muscle group involved an increase in force from zero to maximum over \sim 1–2 s, with the maximal force held for 2–3 s. The force exerted at the wrist was displayed on a monitor and each subject was encouraged to achieve maximal force. There was a 60-s rest between MVC trials. When the peak forces from two of the three trials were not within 5% of each other, additional trials were performed until this was accomplished. The greatest force achieved by the subject was taken as the MVC and, for the elbow flexors, used as the reference to calculate the target level for the brief submaximal contractions and fatiguing contractions. The MVC task with the elbow flexor muscles was also performed at the 5-min time-point during the 20% MVC fatiguing contraction.

For the elbow flexors, a single pulse of electrical stimulation at the predetermined supramaximal level was delivered once the force was at a plateau during the MVC and also 3 s after termination of the MVC while the muscle was at rest.¹ Pilot data indicate that there was no difference in voluntary activation levels when using a single or paired pulse, consistent with results previously reported.¹

EMG Activity and Voluntary Activation during Brief Submaximal Contractions.

The EMG activity and voluntary activation of the involved muscles were recorded in standardized tasks so that the force–EMG relation and force–voluntary activation levels could be compared across days. The standardized tasks involved each subject performing an isometric contraction with the elbow flexor muscles for 6 s at target values of 20%, 40%, 60%, and 80% MVC force, with a 60-s rest between each contraction. A single pulse of electrical stimulation was delivered to the biceps brachii muscle during and after the brief contractions to assess voluntary activation levels during the submaximal contractions. The order of the contractions was randomized across subjects, but remained constant for each subject on the two days.

Fatiguing Contraction.

A fatiguing contraction was performed with the elbow flexor muscles in each experimental session at a target value of either 20% or 80% MVC force. The subject was required to match the vertical target force as displayed

on the monitor and encouraged to sustain the force for as long as possible. The fatiguing contraction was terminated when the force declined by 10% of the target value for 3 of 5 consecutive seconds, despite strong encouragement to maintain force. This time was recorded as the time to task failure. Subjects were not informed of their time to task failure until completion of the second experimental session. Neither the subject nor the investigator who terminated the task knew the time during the tasks.

An index of perceived effort, the rating of perceived exertion (RPE), was assessed with the modified Borg 10-point scale.⁷ Subjects were instructed to focus the assessment of effort on the arm muscles performing the fatiguing task. The scale was anchored so that 0 represented the resting state and 10 corresponded to the strongest contraction that the arm muscles could perform. The RPE was recorded at the beginning of the contraction and every minute thereafter until task failure for the 20% fatiguing contraction. Because of the brevity of the 80% MVC task, subjects were asked their RPE at the beginning of the contraction and at task failure.

Data Analysis.

The torque for the MVC and submaximal contractions was calculated as the product of force and the distance between the elbow joint and the point at which the wrist was attached to the force transducer.

Voluntary activation was quantified by measurement of the force responses to stimulation of the motor nerve.¹³ Any increment in elbow flexion force evoked during a contraction (superimposed twitch) was expressed as a fraction of the amplitude of the control twitch evoked 3 s after the MVC. The level of voluntary activation was derived by the formula: voluntary activation = $100 \times (1 - T_{\text{superimposed}}/T_{\text{control}})$, where $T_{\text{superimposed}}$ was the size of the superimposed twitch and T_{control} was the amplitude of the control twitch produced by stimulation of the motor point in a relaxed but potentiated muscle.¹³

The MVC torque was quantified as the average value over a 0.5-s interval that was centered about the peak. The maximal EMG for each muscle was determined as the root-mean-squared (RMS) value over a 0.5-s interval about the same interval of the MVC torque measurement. The RMS EMG value of the 6-s submaximal contractions for the elbow flexors performed at 20%, 40%, 60%, and 80% of MVC torque was averaged over the 2-s period prior to stimulation during the 6-s contraction. RMS EMG for the biceps brachii, brachioradialis, and triceps brachii muscles was quantified during the fatiguing contraction performed at 20% of MVC at the following time intervals: the first 60 s; 30 s on both sides of 25%, 50%, and 75% of time to task failure; and the last 60 s of the task duration. The RMS EMG during the high-intensity task (80% MVC) was quantified at five continuous intervals equivalent to 20% of the task duration. The EMG activity of the elbow flexor muscles and elbow extensor muscles during the fatiguing contraction was normalized to the RMS EMG value obtained during the MVC for each respective muscle.

The fluctuations in torque during the 20% MVC task were also quantified for the first 60 s; 30 s on both sides of 25%, 50%, and 75% of time to task failure; and the last 60 s of the task duration. The fluctuations in torque during the 80% MVC task were quantified at five continuous intervals equivalent to 20% of the task duration. The amplitude of the torque fluctuations was quantified as the coefficient of variation ($CV = SD/\text{mean} \times 100$).

Statistical Analysis.

Data are reported as mean \pm SD within the text and as mean \pm SE in the figures. Independent *t*-tests were used to compare the characteristics of young and old adults. Analyses of variance (ANOVAs) with repeated measures on a combination of variables, including contraction intensity (20% and 80% MVC), time (0%, 25%, 50%, 70%, and 100% of time to failure), fatigue (pre, 5 min, post), and force (20%, 40%, 60%, and 80% MVC), with age (young, old) as an independent (between subject) factor, were used to compare the various dependent

variables. Dependent variables included the time to task failure, MVC torque, voluntary activation, control twitch amplitude, torque fluctuations, RPE, and RMS EMG for each muscle. Multiple comparisons with Tukey's post hoc tests were used to determine differences among pairs of means. The associations between various variables are reported as the squared Pearson product-moment correlation coefficient (r^2). A significance level of $P < 0.05$ was used to identify statistical significance.

RESULTS

The young adults and old adults differed in age (21.9 ± 3.6 years vs. 70.1 ± 4.3 years, respectively, $P < 0.05$) and height (173.0 ± 8.7 cm vs. 165.7 ± 11.1 cm respectively, $P < 0.05$), but were similar in body mass (69.1 ± 12.3 kg vs. 68.0 ± 18.5 kg). The estimated physical activity levels differed for young (56.0 ± 30.0 MET · hour/week) and old adults (32.5 ± 28.1 MET · hour/week, $P < 0.05$). There was no correlation between the level of physical activity and the change in voluntary activation, change in MVC, or time to task failure.

Time to Task Failure and MVC Torque.

Young adults had a briefer time to task failure than old adults for the 20% MVC fatiguing contraction (14.4 ± 7.5 min vs. 29.5 ± 6.9 min, respectively, $P < 0.05$), but were similar in duration for the 80% task (24 ± 6 s vs. 32 ± 19 s, interaction of contraction intensity \times age, $P < 0.05$).

Young adults were stronger than old adults on both days of testing (63.4 ± 30.4 Nm vs. 43.3 ± 17.8 Nm: pre-fatigue value, main effect of age, $P < 0.05$) and there was no difference in MVC torque between testing days for the young and old adults. MVC torque was reduced from initial values at the end of both fatiguing tasks ($P < 0.05$, Fig. 1). The relative decline in MVC torque was similar for the young and old adults at 5 min into the 20% fatiguing contraction ($22.7 \pm 13.6\%$ vs. $23.0 \pm 16.0\%$, respectively). Immediately after termination of the 20% MVC task, however, the relative reductions in MVC torque from initial values were smaller for young adults than the old ($26.7 \pm 11.7\%$ vs. $37.5 \pm 10.0\%$, respectively, $P < 0.05$). MVC torque was similarly reduced for young and old adults at the end of the 80% MVC task ($15.1 \pm 4.6\%$ vs. $9.3 \pm 14.1\%$, respectively). After the fatiguing contractions, the reductions were greater for the 20% MVC task compared with the 80% MVC task ($32.1 \pm 12.0\%$ vs. $12.4 \pm 11.0\%$, interaction of contraction intensity \times fatigue, $P < 0.05$) for both young and old adults.

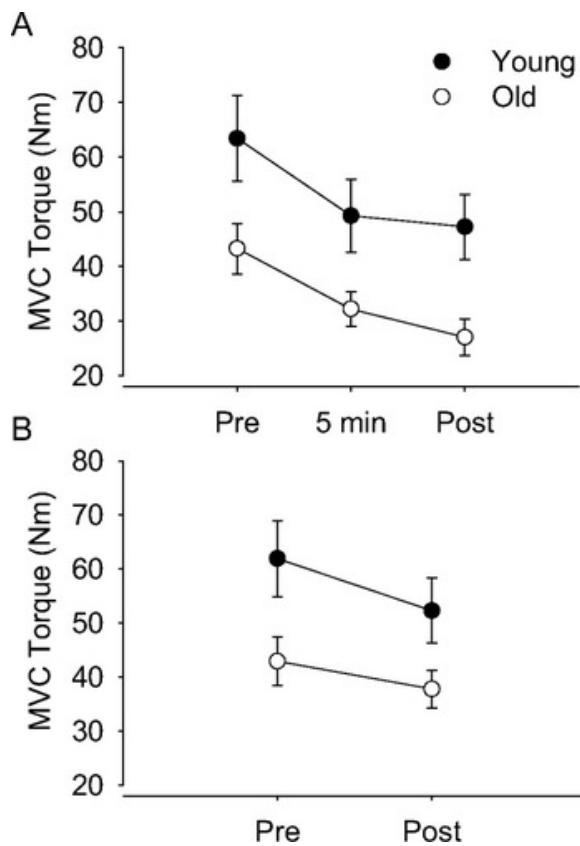


Figure 1 MVC torque of the young and old adults. MVC torque of young and old adults before (pre), at 5 min into (5 min), and after (post) the 20% MVC fatiguing contraction (A) and the 80% MVC task (B). Values are expressed as means (\pm SEM).

Voluntary Activation.

Brief Submaximal Contractions.

The size of the twitch evoked during each of the standardized submaximal contractions performed before the fatiguing contractions on each day decreased and voluntary activation increased similarly for both age groups as the intensity of contraction increased between 20% and 80% of MVC force ($P < 0.05$). The increase in voluntary activation was linear ($P < 0.05$) and similar for each experimental session with no interactions.

Control MVCs.

Before the fatiguing contractions, voluntary activation assessed during control MVCs was greater for young than for old adults (97.8 ± 2.3 vs. $94.2 \pm 3.6\%$, respectively, $P < 0.05$). There was no difference in voluntary activation during control MVCs between the experimental sessions for both age groups. The variability in voluntary activation for each of the MVC trials, however, was greater among the old than young adults ($P = 0.02$; Fig. 2).

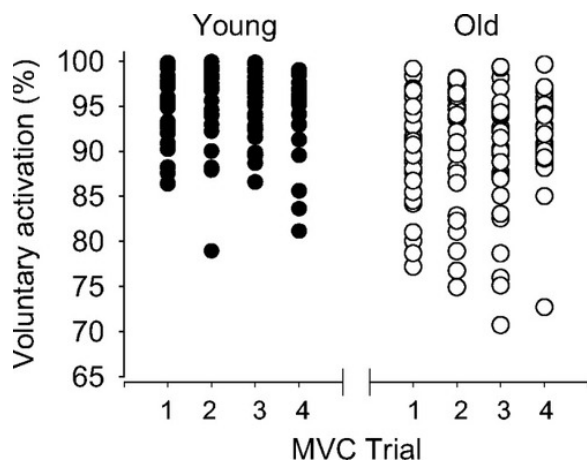


Figure 2 Voluntary activation of the young and old adults during control maximal voluntary contractions (MVC). Voluntary activation, expressed as a percentage, is shown for each subject for the four MVC trials performed before the fatiguing contractions (combined). The range and variability of voluntary activation among the old adults were greater than for the young adults ($P < 0.05$).

Fatigue.

Voluntary activation was reduced at the end of the 20% MVC fatiguing task, but by greater magnitudes for old (to $71.5 \pm 13.9\%$) than young adults (to $84.1 \pm 9.7\%$, $P < 0.05$). The age difference in reductions of voluntary activation occurred between the 5-min assessment and the end of the 20% MVC task (Fig. 3A). Voluntary activation also declined after the 80% task, but to similar levels for young (to $93.6 \pm 5.5\%$) and old adults (to $92.6 \pm 5.1\%$) (Fig. 3B). The reduction in voluntary activation was greater after the 20% MVC task compared with the 80% MVC fatiguing task (interaction of contraction intensity \times task, $P < 0.05$) for both age groups.

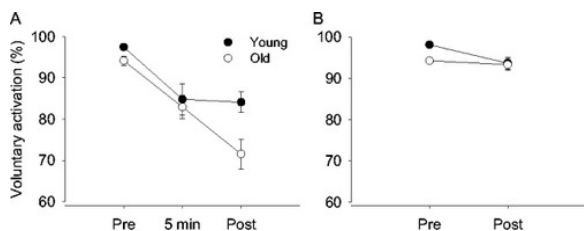


Figure 3 Voluntary activation of the young and old adults before and after the fatiguing contractions. Voluntary activation of young and old adults before (pre), at 5 min into (5 min), and after (post) the 20% MVC fatiguing contraction (A) and the 80% MVC task (B). Values are expressed as means (\pm SEM).

There were significant associations between the change in MVC torque and voluntary activation when assessed immediately after the fatiguing contractions. Those individuals who had greater reductions in voluntary activation experienced a larger decline in MVC torque after the 20% MVC fatiguing contraction ($r = 0.65$, $r^2 = 0.42$, $P < 0.01$; Fig. 4), with significance not reached for the 80% MVC task ($r = 0.35$, $r^2 = 0.12$, $P = 0.06$). When the age groups were analyzed separately, for the 20% MVC task, the association for the young adults was $r = 0.74$ ($r^2 = 0.54$, $P < 0.01$) and $r = 0.44$ ($r^2 = 0.20$, $P = 0.05$) for the old adults.

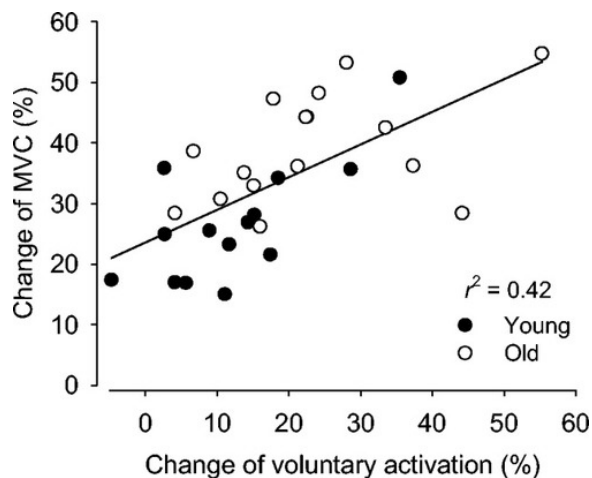


Figure 4 Relation between the change in voluntary activation and change in MVC force for the 20% MVC sustained contraction in young and old adults. Those subjects who had greater changes in voluntary activation had greater changes in MVC when assessed after the low-force fatiguing contraction.

Twitch Amplitude.

The amplitude of the potentiated control twitch torque assessed before the fatiguing contractions was greater for the young than old adults (6.6 ± 1.6 vs. 5.1 ± 2.3 Nm, effect of age, $P < 0.05$) and was similar across experimental sessions. Twitch torque was reduced at the end of both fatiguing contractions for both young and old adults ($P < 0.05$). The decline in twitch torque after the 80% MVC fatiguing contraction was greater for the young ($33 \pm 17\%$) than old adults ($18 \pm 20\%$, interaction of contraction intensity \times age, $P < 0.05$). Old and young adults, however, had similar magnitudes of decline for the 20% MVC task. There was no age difference in the relative decline of twitch torque recorded at 5 min during the 20% MVC fatiguing task for the young and old ($19 \pm 11\%$ vs. $13 \pm 19\%$, respectively) and immediately after the 20% MVC fatiguing task ($28 \pm 13\%$ vs. $33 \pm 18\%$, respectively).

Fluctuations in Torque.

The amplitude of the vertical fluctuations in torque (CV) increased during the 20% and 80% MVC fatiguing contractions (effect of time, $P < 0.05$; Fig. 5). The increase in fluctuations during the 20% MVC task was similar for young ($1.6 \pm 0.5\%$ to $5.7 \pm 1.4\%$) and old adults ($2.1 \pm 1.4\%$ to $5.6 \pm 1.6\%$). However, the rate of change in fluctuations for young adults was greater than for old adults ($0.14 \pm 0.04\%/min$ vs. $0.10 \pm 0.02\%/min$, respectively, $P < 0.05$) during the 20% MVC force fatiguing contraction. During the 80% MVC fatiguing task, the increase and rate of change in fluctuations was similar for young ($2.1 \pm 1.1\%$ to $4.9 \pm 2.1\%$) and old adults ($2.9 \pm 1.4\%$ to $4.2 \pm 1.3\%$, $P > 0.05$).

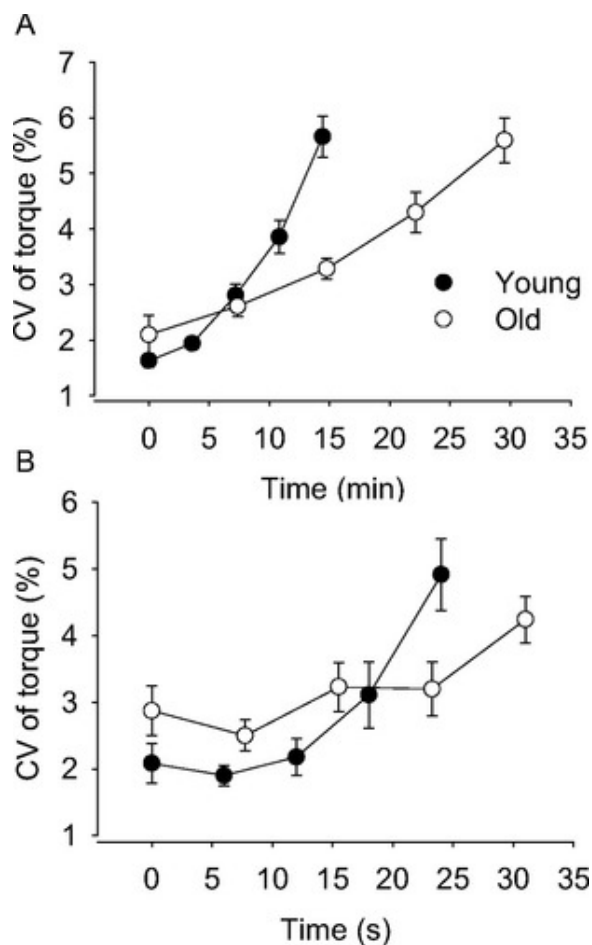


Figure 5 Torque fluctuations for young and old adults during the fatiguing contractions. Coefficient of variation (CV) of torque (%) for the 20% MVC fatiguing contraction is shown at the start and at times corresponding to 25%, 50%, 75%, and 100% of task duration (A) and at intervals equivalent to 20% of task duration for the 80% MVC fatiguing contraction (B). Values are expressed as means (\pm SEM).

EMG Activity.

EMG–Force Relation.

During brief standardized submaximal contractions, EMG activity increased ($P < 0.05$) with contraction intensity on both days in a similar manner for the young and old adults in the biceps brachii and brachioradialis muscles. There was no difference in EMG activity across experimental sessions, nor any interactions of age and contraction intensity.

RMS EMG during Fatiguing Contraction.

The amplitude of the RMS EMG (% MVC) for each of the elbow flexor muscles increased during the 20% and 80% MVC fatiguing tasks ($P < 0.05$; Fig. 6). The amplitude of RMS EMG for biceps brachii in old adults was greater than for young adults during the 20% MVC fatiguing task (effect of age, $P < 0.05$), but not for the 80% MVC. There was a similar trend for the brachioradialis because the effect of age was $P = 0.057$ for the 20% contraction, with no difference between age groups for the 80% MVC task. The amplitude of RMS EMG for triceps was similar between young and old adults for the both 20% and 80% MVC fatiguing contraction.

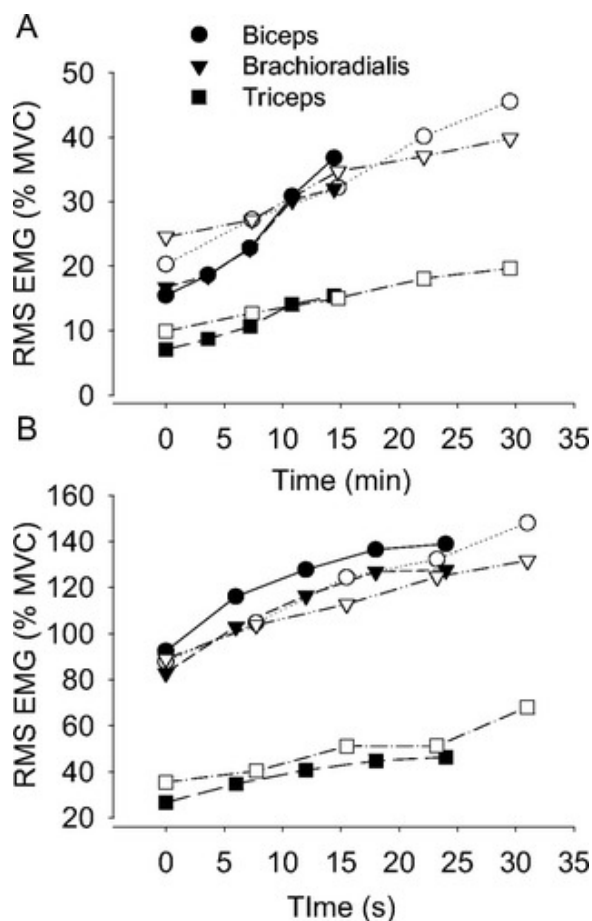


Figure 6 RMS EMG normalized to the MVC values (% MVC). RMS EMG for the 20% MVC fatiguing contraction is shown at the start and at times corresponding to 25%, 50%, 75%, and 100% of task duration (**A**), and at intervals equivalent to 20% of task duration for the 80% MVC fatiguing contraction (**B**). Filled symbols: young adults; open symbols: old adults. Values are expressed as means.

Perceived Exertion during the Fatiguing Contractions.

The RPE increased during both fatiguing contractions ($P < 0.05$). RPE was similar for the young and old adults at the beginning (2.1 ± 1.2 vs. 2.2 ± 1.1 , $P > 0.05$) and end (10.0 ± 0.1 vs. 10.0 ± 0.0) of the fatiguing contraction for the 20% MVC task. However, the rate of increase in the RPE was more gradual for old than young adults ($0.6 \pm 0.2/\text{min}$ vs. $0.3 \pm 0.1/\text{min}$, $P < 0.05$) during the 20% MVC task. The RPE was similar at the start and finish of the 80% MVC task for the young and old adults.

DISCUSSION

We found that old adults exhibited marked and greater declines in voluntary activation than young adults at the end of a 20% MVC fatiguing contraction, but the reductions in voluntary activation were similar for the two age groups after the 80% MVC task. Changes in voluntary activation contributed to the relative decline in MVC torque after the low-force fatiguing contraction. Twitch amplitude was reduced more for young than for old adults after the 80% MVC task, but was reduced to similar levels for each age group during and at termination of the 20% MVC task. The time to failure for the sustained isometric contraction was longer with age for the 20% MVC task despite old adults exhibiting greater central fatigue immediately after the task. In contrast, young and old adults had a similar time to failure for the 80% MVC task.

The longer time to task failure with increased age for the low-force fatiguing contraction is consistent with other studies.^{5, 20, 23} In contrast, the time to failure was similar between young and old adults for the high-intensity fatiguing task. The age and task differences in time to failure were not due to varying levels of effort because RPEs were similar at the end of each contraction for both age groups. We also found that there was no association between physical activity levels and time to failure or any other measure of fatigue, which is consistent with previous studies.²³ The measure of physical activity in our study, however, was not specific to the upper limb. It is possible, therefore, that an age-related difference in the activity level of upper limbs may influence muscle phenotype and fatigue resistance of elbow flexor muscles. When young and old men were matched for strength and reported similar physical activity levels, the old men had a longer time to task failure than the young men for a low-force, sustained contraction.²³ The lack of age difference in fatigability for high-force isometric fatiguing contractions has been also observed in other studies for various muscle groups^{17, 35, 45} but not for maximal contractions,^{9, 22, 34} which involved greater decrements in MVC force than the 80% MVC task induced in the present study.

Both the young and old adults exhibited impairment within the central nervous system and the muscle fibers that contributed to neuromuscular fatigue after both tasks. For the 80% MVC task, there was no difference in time to failure with age, but the reduction in twitch amplitude was smaller for the old adults than the young. The change in twitch amplitude represents changes in excitation–contraction coupling and is due to the interaction of the processes that mediate potentiation and fatigue within the muscle.^{15, 37} Twitch potentiation is lower in old than in young adults.^{3, 19} Age differences in potentiation, therefore, do not explain the smaller reduction in twitch amplitude after the 80% MVC task for the old adults, although they may have contributed to the similar reductions with age in twitch amplitude after the 20% MVC task. These results are consistent with a different proportional area of fiber types in the elbow flexors for the two age groups because the old muscle was less fatigable. Old adults usually have a greater proportion of type I area than young adults in the biceps brachii muscles^{29, 30} due to age-related loss of large motor units.¹¹ Consequently, old adults have a more oxidative metabolic profile,^{26, 27} with greater reliance on non-oxidative sources of adenosine triphosphate (ATP) during a fatiguing contraction²⁷ and slower contractile properties.^{10, 22} These age-related changes in the muscle likely explain the longer time to task failure of the old adults for the 20% MVC task compared with the young adults.

Central mechanisms contributed to task failure and the reduction in MVC force during the low-force fatiguing contraction (at the 5-min time-point) and at the end of the low- and high-force fatiguing contractions. The loss of voluntary activation indicated that either the motor units were not all recruited voluntarily or they were discharging at rates that were not high enough to produce full fusion of force.¹⁸ There were greater reductions in voluntary activation, however, after the 20% MVC task, which induced greater muscle fatigue than the 80% task for both young and old adults. The reductions in voluntary activation immediately after the low-force task paralleled the relative change in MVC force. Accordingly, there was an association between the reduction in voluntary activation and the change in MVC force for the 20% MVC, indicating central fatigue contributed to muscle fatigue for both the young and old adults. The time course of change in voluntary activation, however, may have differed with age. To fully understand whether the rate of decline in voluntary activation and development of central fatigue differs with age, voluntary activation needs to be assessed at the same time in young and old adults during contraction at several time-points.

The old adults were more impaired in force production at the termination of the 20% MVC task than the young adults, despite marked and similar declines at 5 min into the task. The greater muscle fatigue for the old adults is largely explained by an age-related loss of voluntary activation. The increased central fatigue with age during recovery of the elbow flexor muscles during a sustained contraction has been in part attributed to supraspinal fatigue,²² which is due to suboptimal output from the motor cortex.⁴⁷ Age-related changes in the central nervous

system, such as degradation of the cortical neuron and motoneuron^{8,36} and reduced excitability of the motor cortex and motoneuron pool,^{40,43} may predispose old adults to greater impairment of neural drive to the muscle and force production during a fatiguing contraction.

Age-related increased central fatigue has been shown for isometric fatiguing contractions with the elbow flexor and quadriceps muscles,^{5, 6, 22, 46} but not after intermittent contractions or contractions with lower-leg muscles.^{2, 4} We also found similar reductions of voluntary activation with age after the 80% MVC task, which induced a smaller decline in MVC force compared with after the 20% MVC task. These results and recent findings²² indicate that, at least for the elbow flexor muscles, age-related increases in central fatigue are greatest during recovery from contractions that induce large magnitudes of muscle fatigue. The different findings between studies and contraction intensities in the magnitude of central fatigue with age, therefore, may be a product of the magnitude of fatigue induced by the sustained contractions or the involved muscles.

EMG activity during the low-force, sustained contraction was greater for the old than for young adults for the elbow flexor muscles. The increase in EMG activity is largely due to the recruitment of larger motor units as the muscle becomes progressively fatigued.¹⁴ Thus, the old adults appeared to activate a greater portion of the motor unit pool of the biceps and brachioradialis muscles than young adults during the low-force fatiguing contraction. The age difference in EMG activity was not due to recording conditions, because EMG activity was similar for the young and old adults during brief non-fatiguing submaximal contractions at varying intensities. Furthermore, the differences in EMG were not due to antagonist activity of the triceps brachii, which was similar during the fatiguing contraction for the young and old adults. Synergistic activity of the agonist muscles contributing to elbow flexion force, however, may have differed between groups. For example, the EMG activity of the brachialis muscle was not measured in this study and it contributes significantly to elbow flexion force.²⁰ Brachialis muscle activation can differ in a motor task between young and old adults¹⁶ and with age during an isometric fatiguing contraction,²⁰ potentially offsetting activation of the biceps brachii and brachioradialis muscle in the old adults. The age difference in activation strategies with fatigue may have contributed to the greater reduction in voluntary activation and MVC force in the old adults. Accordingly, for the 80% MVC task, the elbow flexor muscles of the young and old adults had similar muscle activation levels and similar reductions in MVC force, voluntary activation, and task duration. At this higher intensity of contraction, many of the motor units are recruited³² for young and old adults, indicating that alternative recruitment strategies were limited in influencing time to task failure.

At the start of the isometric contractions, the old adults had greater fluctuations in torque than the young adults¹² and was in part due to a more variable discharge rate of the active motor units in old adults.³³ The young adults had a higher rate of increase in fluctuations of torque than the old adults as fatigue developed during the low-force, sustained contraction, which probably reflects a more rapid rate of recruitment of motor units that have greater discharge rate variability at higher forces³⁸ during the task. The change in fluctuations, however, was consistent with the rates of increase in EMG activity for low- and high-force tasks in the young and old adults studied herein.

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Abbreviations

ANOVA, analysis of variance; CV, coefficient of variation; EMG, electromyography; MVC, maximal voluntary contraction; RPE, rating of perceived exertion; RMS, root mean squared

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