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Age-related fatigability of the ankle dorsiflexor muscles during concentric and eccentric contractions

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Abstract This study compares the fatigability of the ankle dorsiflexors during five sets of 30 maximal concentric and eccentric contractions in young and elderly adults. The torque produced by the ankle dorsiflexors and the average surface electromyogram (aEMG) of the tibialis anterior were continuously recorded. The contribution of central and peripheral mechanisms to muscle fatigue was tested before, after each set of contractions, and during a 30 min recovery period by the superimposed electrical stimulation method. The compound muscle action potential (M-wave), the mechanical response to single (twitch) and paired (doublet) stimulation, and the postactivation potentiation were also recorded. Compared with young subjects, elderly adults exhibited a greater loss of torque for concentric (50.2 vs. 40.9%; $P < 0.05$) and eccentric (42.1 vs. 27.1%; $P < 0.01$) contractions. Although young subjects showed a lesser decrease in torque during the eccentric compared with concentric contractions, elderly adults experienced similar fatigability for the two types of contractions despite a comparable depression in the EMG activity of both groups and contraction types (10–20%). As tested by the interpolated-twitch method and aEMG/M-wave ratio, voluntary activation was not altered during either type of contraction or for either age group. During the two fatigue tasks, only elderly adults experienced a decrease in M-wave area (26.4–35.4%; $P < 0.05$). All together, our results suggest that the fatigue exhibited by both young and elderly adults during maximal concentric and eccentric contractions mainly involved peripheral alterations and that elderly adults may also have experienced a decline in neuromuscular propagation.

Keywords Muscle fatigue · Electromyography · Ageing · Voluntary contraction · Excitation–contraction coupling

Introduction

Despite the extensive literature on neuromuscular fatigue, the effects of ageing on the mechanisms of task failure have been less studied and appear to be equivocal (Allman and Rice 2002). In addition to a possible difference in the physical capabilities of the subjects among studies, one possible explanation for this lack of consensus is the well-known concept of task-dependency (Enoka and Stuart 1992; Gandevia 2001). For example, it has been reported that elderly are less prone to fatigue than young adults during submaximal sustained voluntary contractions (Hunter et al. 2004), incremental isometric contractions (Kent-Braun et al. 2002), and intermittent maximal voluntary contractions (MVC; Ditor and Hicks 2000). In contrast, Allman and Rice (2001) did not find any difference in fatigability between age groups during intermittent submaximal voluntary contractions. Among the few studies that have investigated age-related fatigability during dynamic contractions, most have reported a similar degree of fatigue resistance in young and elderly adults (Laforest et al. 1990; Larsson and Karlsson 1978; Linstrom et al. 1997). Recently, however, Lanza et al. (2004) reported a reduced susceptibility to fatigue during concentric contractions with the ankle dorsiflexor muscles, whereas Petrella et al. (2005) found an increased fatigability in elderly subjects compared with young adults during maximal dynamic knee extensions.

These divergent results could have been influenced by several parameters. For example, ageing is associated with a general shift toward a greater proportion of slow and fatigue-resistant (type I) muscle fibres (Jakobsson et al. 1988) that should improve the endurance capacity of the muscle. However, the degree of fatigue that occurs during a submaximal sustained contraction is also af-

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affected by the total muscle mass and thereby, the level of intramuscular pressures and blood flow occlusion during the contraction (Hunter et al. 2001; Russ and Kent-Braun 2003). Even though ageing is accompanied by a substantial reduction in muscle mass and strength, it has been reported however, that the increased ability of elderly adults to sustain a relative submaximal force cannot be attributed to a reduced impediment to muscle perfusion (Hunter et al. 2005), as it is the case when young women and men are compared (Hunter and Enoka 2001; Russ and Kent-Braun 2003). Nevertheless, the relative importance of this mechanism could be specific to the muscle group investigated as the reduction in maximal force that occurs during ageing differs between muscles and modalities of contraction (isometric, concentric and eccentric; see Klass et al. 2005; Lanza et al. 2004; Vandervoort 2002). Superimposed on these effects, ageing may involve a reduced ability of the central nervous system to activate the agonist muscles (Stackhouse et al. 2001) due to the reorganisation of areas in the brain and the remodelling of motor units that is known to accompany the decline in muscle strength (Vandervoort 2002).

No study has compared the neuromuscular fatigue that occurs during maximal concentric and eccentric contractions and assessed the underlying mechanisms in elderly adults. Such an investigation is of particular interest because the maximal torque that elderly adults can produce is preserved more during eccentric contractions compared with concentric contractions (Klass et al. 2005). The purpose of this study was to investigate the age-related changes in fatigability of the ankle dorsiflexor muscles during repeated maximal concentric and eccentric contractions and the time course of their recovery. The main objective was to evaluate the relative contribution of central and peripheral mechanisms to the force decay and to examine age and sex differences.

Materials and methods

Sixteen young subjects (eight women) aged between 22 and 47 years (mean \pm SD: 30.5 \pm 2.5 years) and 16 elderly adults (eight women) aged between 72 and 87 years (77.2 \pm 1.4 years) volunteered to participate in this study. All subjects were healthy and reported no neuromuscular disorders. Elderly persons were living at home and walked daily without using any assistive device. All subjects participated in three sessions: first, for familiarization and second, for data collection, with one session involving maximal concentric contractions and the other maximal eccentric contractions. Subjects practiced the two types of contractions and experienced the electrical stimulation during the familiarization session. The two fatigue tests were separated by at least 1 week. As lengthening of contractions are known to induce muscle damage that recovers slowly (Clarkson and Newham 1995), the test involving maximal concentric contractions was always performed first.

Subjects did not engage in any strenuous locomotor activity for at least 24 h before the experimental sessions. Each subject gave informed consent prior to participation in this study. The experimental procedures were approved by the local Ethics Committee and performed in accordance with the Helsinki Declaration.

Mechanical and EMG recordings

Each subject sat on an adjustable chair in a slightly reclined position with the right foot strapped to a footplate of an ankle ergometer described previously (Pasquet et al. 2000). The plate was inclined at an angle of 45° to the floor and the seat was adjusted so that the ankle joint was at a right angle (neutral position). The foot was held in place by a heel block and secured to the plate via two straps. One strap was placed around the foot, 1–2 cm proximal to the metatarsophalangeal joint of the toe, and the second strap was placed around the foot just below the ankle joint. The isometric torque of the dorsiflexor muscles during MVCs or electrical stimulations were recorded by strain-gauge transducers (sensitivity: 0.018 V/Nm; linear range: 0–200 N m) that were mounted on the rotational axis of the motor.

The surface EMG was recorded from the tibialis anterior by means of two silver disk electrodes (8 mm in diameter). The first electrode was placed over the muscle belly, at the proximal one-third of the distance between the neck of the fibula and the lateral malleolus. The second electrode was positioned 2 cm below the first one. The ground electrode (2 \times 3 cm silver plate) was fixed in between the stimulating electrode and the EMG electrodes. The EMG signals were amplified (1,000x) and filtered (10 Hz–5 kHz) by a custom-made differential amplifier. The torque and the EMG signals were simultaneously recorded by a computer at a sampling rate of 2 kHz and analysed off-line by using the Acq-Knowledge data analysis software (Model MP150; Biopac System Inc., Santa Barbara, CA, USA).

Stimulation procedure

The contraction of the dorsiflexor muscles was induced by rectangular electrical pulses (0.2 ms in duration) delivered by a custom-made stimulator triggered by a digital timer (model 4030; Digitimer Ltd., Welwyn Garden City, UK). The stimuli were delivered through two silver disk electrodes (8 mm diameter), with the cathode attached to the skin over the deep peroneal nerve near the neck of the fibula and the anode placed on the opposite side of the leg (Klass et al. 2005). Maximal electrical stimulation was determined by progressively increasing the intensity until the compound muscle action potential (M-wave) and the corresponding torque reached a plateau. The level of stimulation was then set 10–20% above maximum. Care was taken to

avoid activation of the peroneal muscles, and the absence of muscle activity was checked by palpation and analysis of the mechanical twitch. Any deflection of the mechanical trace under the baseline was interpreted as antagonist muscle activity. The degree of the dorsiflexor muscles activation during voluntary contraction was assessed by the twitch-interpolation method (Belanger and McComas 1981) by using paired supramaximal pulses at 10 ms interval (100 Hz).

Experimental procedure

In addition to the familiarization session, each subject performed about 20–30 submaximal contractions (~ 10 –20% of maximum) at the beginning of each experimental session to reinforce the timing of the duty cycle. Then each subject performed one or two MVCs with superimposed paired stimulation to verify that the contraction was maximal. The fatigue test involved five sets of 30 maximum voluntary concentric or eccentric contractions with the dorsiflexor muscles. Each set of 30 contractions was separated by a 1 min pause. The contractions were performed over a 30° range of motion (from 30° plantarflexion to 0° and from 0° to 30° plantarflexion for concentric and eccentric contractions, respectively) at a constant angular velocity (50°/s) and at the rate of one contraction every 3.5 s. The subjects were required to produce an MVC under isometric condition just before the footplate was rotated (Komi et al. 2000). To help them, they were provided with visual feedback of the torque and displacement signals on a digital oscilloscope (model 120; Nicolet, Madison, WI, USA), and the exact timing for contraction and relaxation was given by one of the investigators. The subjects were verbally encouraged to exert maximal force throughout the entire range of motion.

The mechanical and electrical responses of the muscle, for both electrically induced and voluntary isometric contractions, were recorded with the foot held in a neutral position before, between each of the five sets of contractions, and after 5, 10, 15, and 30 min of rest. After the last contraction of each set, single and a paired stimuli were delivered to the nerve at 5 s, the subject performed an isometric MVC with superimposed paired electrical stimulation (interpolated-twitch method) at 20 s, and a double stimulation (P_d) was applied 2 s after the end of the MVC. After each MVC, the footplate was passively returned to the starting position prior to the next set of concentric or eccentric contractions.

Measurements

The average value of the torque and aEMG developed throughout the entire range of motion (0.75 s) were measured for each concentric and eccentric contraction during the fatigue test (Pasquet et al. 2000). The torque and the associated aEMG amplitude were also

measured for a 1 s period before the paired supra-maximal pulses during the torque plateau of the isometric MVC.

The following parameters were measured from the electrically induced responses: peak torque of the single (P_t), paired (P_d) responses and corresponding contraction time (CT) and time to half-relaxation ($TR_{1/2}$). Maximal rate of torque development ($+dP_t/dt$ or $+dP_d/dt$) and relaxation ($-dP_t/dt$ or $-dP_d/dt$) were obtained from the first derivative of the force signal. Although, P_t is a global measure of the excitation–contraction coupling, the twitch time course is intended to assess indirectly changes in Ca^{2+} release ($+dP_t/dt$ and CT) and re-uptake by the sarcoplasmic reticulum and/or dissociation of Ca^{2+} from troponin ($-dP_d/dt$ and $TR_{1/2}$). Postactivation potentiation, determined by computing the ratio between the size of P_d recorded before and after the isometric MVC, was taken as an indicator of myofibrillar Ca^{2+} sensitivity (Grange and Houston 1991; Sweeney et al. 1993). The compound muscle action potential (M-wave) was used to assess the excitability of the neuromuscular junction and sarcolemma, and neuromuscular propagation. The M-wave was characterised by peak-to-peak amplitude, total duration, and area. The size of the superimposed double response was expressed as a percentage of the one obtained in the resting muscle and this percentage was then subtracted from 100% to provide a quantitative measure of central activation (Gandevia 2001). The aEMG during the voluntary dynamic contractions was computed from the last five repetitions of each set and normalised to that of the M-wave recorded immediately after each set of contractions to provide another indirect measure of the subjects' capacity to activate the muscle.

Statistics

A four-factor ANOVA (age \times sex \times contraction type \times time) with repeated measures on time and contraction type was used to compare the data collected during the two fatigue tests. Because no interaction ($P > 0.05$) was obtained for sex, all data were analysed by means of a three-factor ANOVA (age \times contraction type \times time) with repeated measures on time and contraction type. When a significant main effect was found, a Dunnett post-hoc test was used to identify the significant differences over time between selected means and control values and a Student–Newman–Keuls post-hoc test was used to compare age groups and contraction types. $P < 0.05$ was considered significant. Data are given as mean \pm SE.

Results

The torque produced by the dorsiflexor muscles during an isometric MVC was greater for young adults (38.3 ± 3.1 N m; collapsed across sex) compared with elderly adults (28.6 ± 1.3 N m; $P < 0.001$). The aver-

age torque during maximal concentric contractions was lower than that during maximal eccentric contractions for both young (23.4 ± 2.6 vs. 45.7 ± 3.6 N m; $P < 0.001$) and elderly adults (14.4 ± 1.1 vs. 36.5 ± 2.1 N m; $P < 0.001$). In contrast, there was no group \times contraction type interaction ($P > 0.05$) for voluntary aEMG activity of the tibialis anterior (data not shown).

The twitch and doublet responses to electrical stimuli differed between young and elderly adults of both sexes (Table 1), with a marked slowing of the contractile kinetics for the elderly adults. These mechanical adaptations were associated with a lower peak-to-peak amplitude ($P < 0.05$) and longer dura-

tion ($P < 0.05$) of the M-wave for the elderly (2.7 ± 0.8 mV and 6.3 ± 0.7 ms, respectively) compared with young adults (3.2 ± 0.3 mV and 4.6 ± 0.3 ms). In contrast, the M-wave area did not differ significantly between young ($11.3 \pm 3.4 \mu\text{V s}^{-1}$) and elderly adults ($10.6 \pm 1.5 \mu\text{V s}^{-1}$).

Torque and EMG activity during fatiguing contractions

In the absence of a significant interaction ($P > 0.05$) between the decline in torque during fatigue and sex, the data on women and men were pooled. As illustrated in Fig. 1, torque declined progressively during each set of

Table 1 Mechanical responses to single (twitch) and paired (doublet) stimulation in young and elderly adults in control conditions

	Torque (N m)	CT (ms)	TR _{1/2} (ms)	+dTorque/dt (N m/s)	-dTorque/dt (N m/s)
Twitch					
Young	1.8 ± 0.1	80.6 ± 2.4	68.3 ± 2.7	42.2 ± 2.4	25.8 ± 1.5
Elderly	2.0 ± 0.2	$102.5 \pm 2.7^*$	$80.6 \pm 3.0^*$	$32.7 \pm 2.3^*$	$21.3 \pm 1.4^*$
Doublet					
Young	6.3 ± 0.4	97.4 ± 2.2	78.7 ± 2.3	123.2 ± 9.7	85.9 ± 7.8
Elderly	5.7 ± 0.4	$126.6 \pm 2.7^*$	$97.1 \pm 3.1^*$	$90.4 \pm 7.8^*$	$53.1 \pm 3.4^*$

Values are means \pm SE ($n = 16$)

CT contraction time, TR_{1/2} half time of relaxation, +dTorque/dt maximal rate of torque development, -dTorque/dt maximal rate of torque relaxation

*Denotes significant difference ($P < 0.05$) between groups

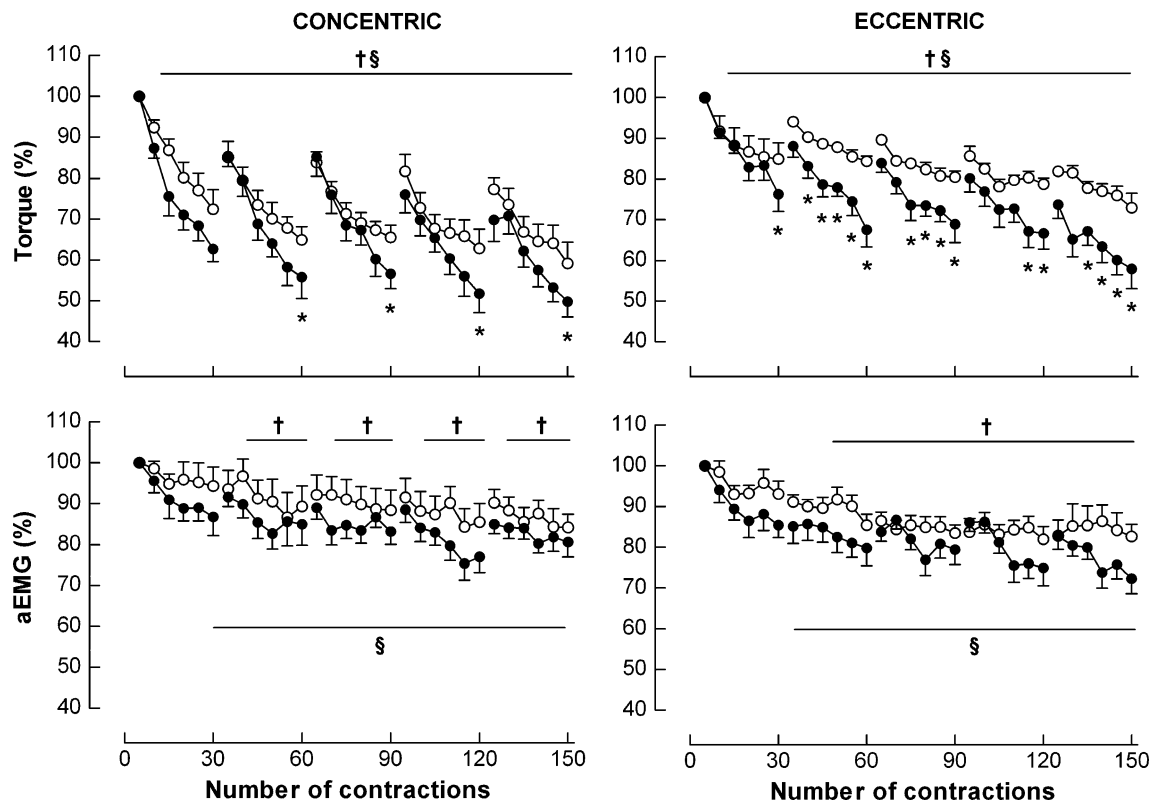


Fig. 1 Comparison of changes in torque and aEMG during the fatigue tests involving maximal concentric and eccentric contractions in young (open circles) and elderly (filled circles) groups. Data, expressed as percentage of initial values, are means \pm SE for 16

subjects in each group. Each data point corresponds to the average of five successive contractions for each individual. Significant difference ($P < 0.05$): * between young and elderly adults; § and † with control values for young and elderly adults, respectively

repeated maximal concentric and eccentric contractions in both groups, but the decrease was greater in the elderly adults (age \times time interaction, $P < 0.05$). The difference in the reduction in torque between the two age groups increased with the number of repetitions during the maximal eccentric contractions. After each set of 30 contractions, the decline in torque during the maximal eccentric contractions was less than during the concentric contractions (Student–Newman–Keuls test, $P < 0.05$) for the young subjects, but not for the elderly subjects. At the end of the fatigue test, the torque decreased by 40.9% for the young subjects and 50.2% for the elderly subjects ($P < 0.05$) for the concentric contractions, and by 27.1 and 42.1% ($P < 0.01$) for the young and elderly adults respectively, during the eccentric contractions. The associated aEMG decreased significantly (main effect, $P < 0.05$) throughout the two fatigue tasks (Fig. 1) but similarly (age \times contraction type \times time interaction, $P > 0.05$) for the two groups of subjects.

Voluntary isometric MVC after fatiguing contractions

The isometric MVC torque recorded during the brief rest period between successive sets decreased progressively during both fatiguing tests and in both groups of

subjects (Fig. 2). There was no statistical difference between groups or contraction types. After 30 min of recovery, however, the torque deficit was greater (contraction type \times time interaction, $P < 0.05$) after the test that involved eccentric contractions (26.2 and 28% for young and elderly adults, respectively) compared with the test involving concentric contractions (14.9 and 14.5% for young and elderly adults, respectively).

These changes in isometric MVC torque were accompanied by a significant reduction of the aEMG (main effect, $P < 0.05$) without any statistical difference between young and elderly adults for either type of contraction (Fig. 2). The time-course of EMG recovery differed (contraction type \times time interaction, $P < 0.05$) after the two fatigue tests. Thirty minutes after completing the fatigue test involving maximal eccentric contractions, the aEMG deficit was 20.7 and 11.9% (Dunnett test, $P < 0.01$) for young and elderly adults, respectively. In contrast, the aEMG recovered within 5 min after the test with concentric contractions for the elderly adults, whereas young adults exhibited a deficit throughout the recovery period ($P < 0.05$). At the end of the recovery period, the deficit in aEMG after the concentric contractions (13.3 and 4.9% for young and elderly adults, respectively) was significantly less (Student–Newman–Keuls test, $P < 0.001$) than that after the eccentric contractions.

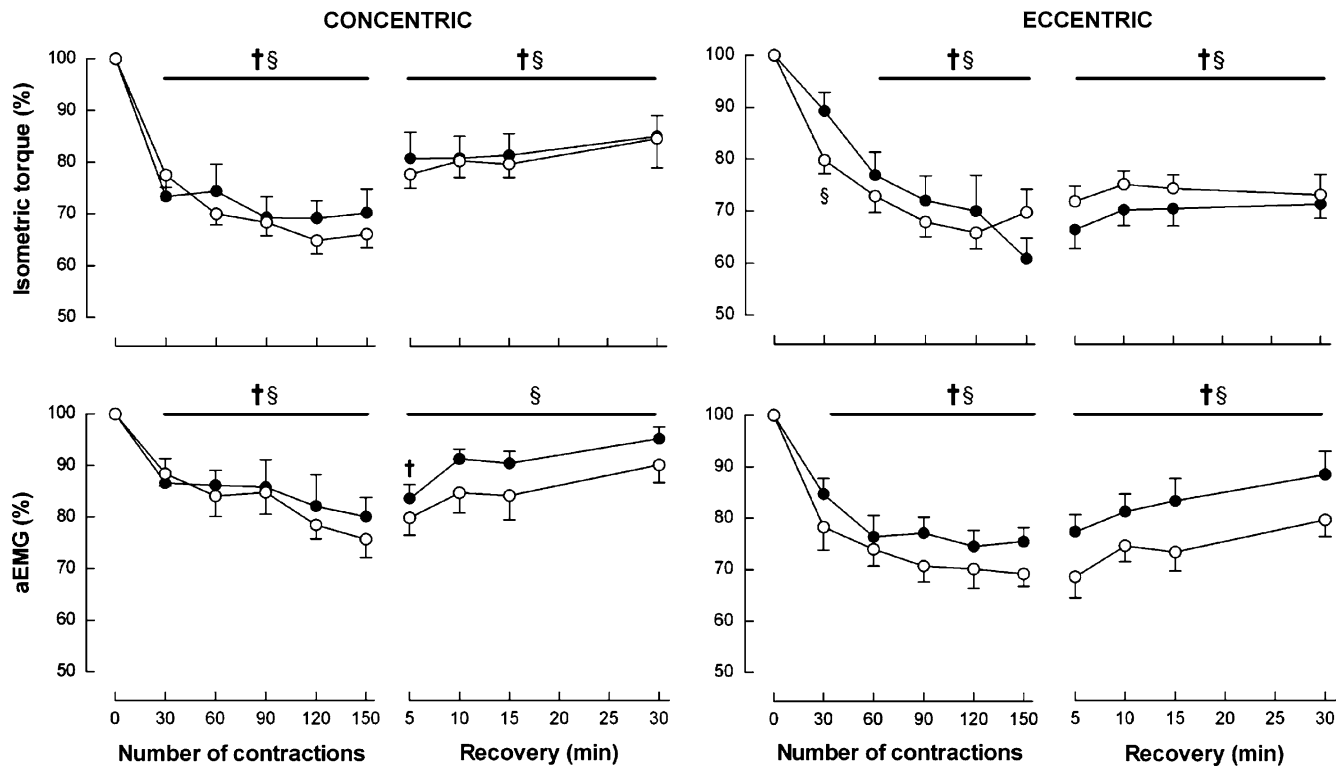


Fig. 2 Comparison of the changes in isometric MVC torque and aEMG during the fatigue tests involving maximal concentric and eccentric contractions in young (*open circles*) and elderly (*filled circles*) groups. Data, expressed as percentage of initial values, are

means \pm SE for 16 subjects in each group. § and † denote significant difference ($P < 0.05$) with control values for young and elderly adults, respectively

Voluntary activation

The interpolated-twitch method indicated that the neural activation of the muscle was maximal for all young and elderly subjects in control conditions, throughout the course of the two fatigue tasks, and their recovery period (data not illustrated). The absence of a change in voluntary activation during the fatiguing contractions is consistent with the EMG data. For both fatigue tasks, the amplitude of the aEMG activity recorded during both fatiguing contractions, normalised to that of the M-wave, did not change significantly at the end of each set of contractions either in young or elderly adults (Fig. 3).

Contractile and electrical muscle properties during fatiguing contractions

Figure 4 illustrates the changes in the twitch parameters during the two fatigue tasks. For young adults, P_t potentiated after the first set of contractions in both fatigue tasks with a more pronounced effect (contraction

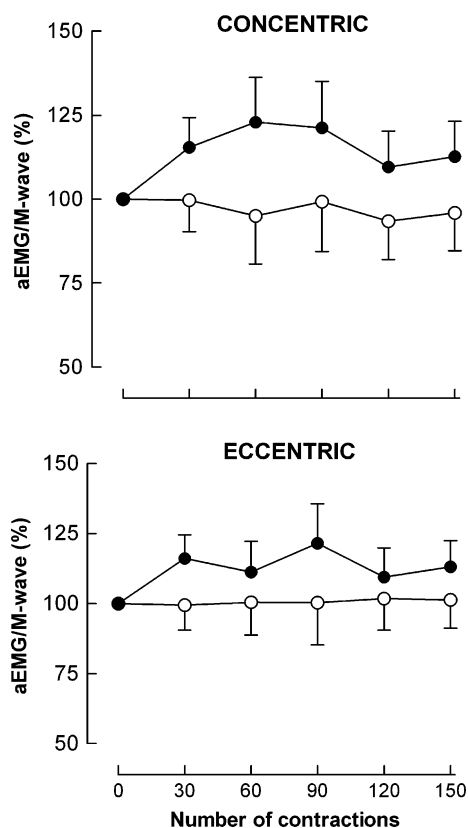


Fig. 3 Comparison of aEMG/M-wave area ratio during the fatigue tests involving maximal concentric and eccentric contractions in young (open circles) and elderly (filled circles) groups. Data, expressed as percentage of initial values, are means \pm SE for 16 subjects in each group. For each ratio, the aEMG was computed from the last five fatiguing contractions of each set and normalised to that of the M-wave recorded immediately after each set of contractions

type \times time interaction, $P < 0.01$) for the test with eccentric contractions (78.4%; $P < 0.01$) compared with the concentric contractions (28.9%; $P < 0.01$). P_t remained significantly potentiated until the fourth set ($P < 0.01$) during the test with eccentric contractions, whereas it declined progressively after the first set of concentric contractions and reached lower values ($P < 0.05$) than in pre-fatigue condition at the end of the test. The contractile kinetics ($+dP_t/dt$ and $-dP_t/dt$) followed the same pattern of changes than for P_t (data not shown). At the end of the fatiguing contractions and throughout the recovery period, P_t , $+dP_t/dt$ and $-dP_t/dt$ were similarly and significantly reduced (Dunnett test, $P < 0.05$) in both fatigue tasks. After 30 min of recovery, P_t was still reduced by 36.2% ($P < 0.01$) during the test with concentric contractions, and by 44.6% ($P < 0.01$) during the test with eccentric contractions.

In contrast, the twitch did not potentiate and declined similarly during the two fatigue tasks in the elderly group. After the five sets of contractions, P_t , $+dP_t/dt$ and $-dP_t/dt$ were reduced (Student–Newman–Keuls test, $P < 0.01$) by 57.4, 37.1, and 48.5% in the concentric task, and by 61.7, 47.2, and 37.3% in eccentric task, respectively. The recovery was similar to that of young adults as there was no difference between groups during the recovery period, except after 5 min of rest in the eccentric task.

CT decreased in both groups during the two fatigue tasks with a more pronounced effect during the eccentric contractions for the elderly adults compared with young adults (age \times contraction type \times time interaction, $P < 0.01$; Fig. 4). Although CT recovered quickly after the two fatigue tasks for the young adults and after the concentric task in elderly adults, this parameter remained depressed during the first 15 min of the recovery after eccentric contractions for elderly adults. $TR_{1/2}$ showed a different pattern of change by increasing at the beginning of the test involving concentric contractions in both groups before returning progressively to pre-fatigue values at the end of the test. In contrast, both age groups displayed a significant ($P < 0.05$) decrease in $TR_{1/2}$ at the end of eccentric task. For both groups, $TR_{1/2}$ recovered to initial values after 5 min following the concentric contractions, whereas it remained below the initial values ($P < 0.05$) during the 30 min of recovery after the eccentric contractions.

Although there was no significant difference M-wave amplitude and area for the young adults during the two fatigue tasks, this parameter showed a significant reduction in elderly adults (age \times time interaction, $P < 0.05$; Fig. 5). At the end of the fifth set of contractions, M-wave peak to peak amplitude and area were reduced in the elderly, respectively, by 27.6 ± 12.0 and $26.4 \pm 8.7\%$ (Dunnett test, $P < 0.01$) for the concentric contractions, and by 25.6 ± 9.8 and $35.4 \pm 7.9\%$ ($P < 0.01$) for the eccentric contractions. After both fatigue protocols, the M-wave recovered its initial values within 5 min of rest. These changes were

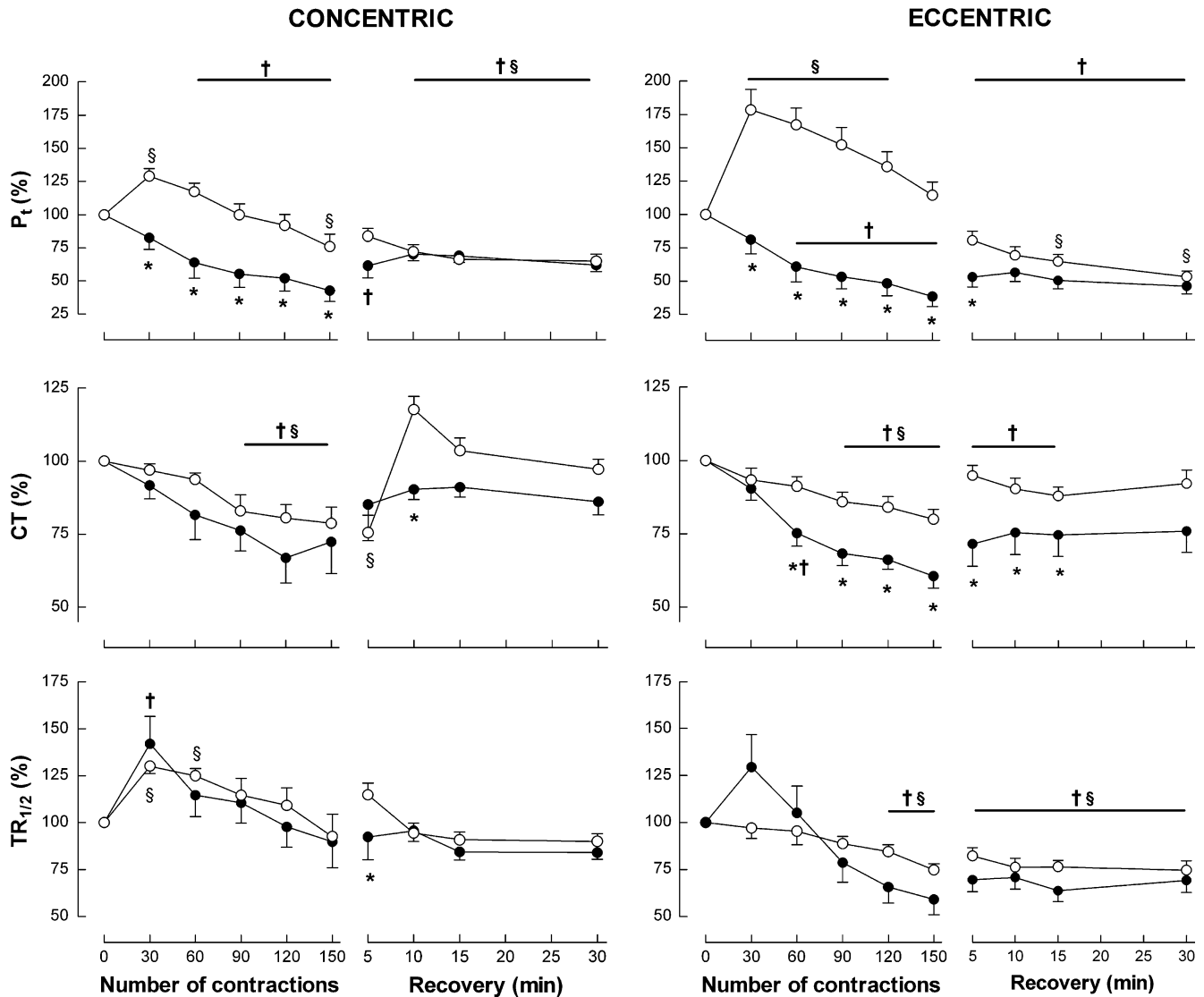


Fig. 4 Comparison of changes in twitch parameters during the fatigue tests involving maximal concentric and eccentric contractions in young (open circles) and elderly (filled circles) groups. Data, expressed as percentage of initial values, are means \pm SE for 16 subjects in each group. Parameters compared are (from top to

bottom): twitch torque (P_t), contraction time (CT), and half-relaxation time ($TR_{1/2}$). Significant difference ($P < 0.05$): * between young and elderly adults; § and † with control values for young and elderly adults, respectively

largely due to a reduction in amplitude as M-wave duration did not differ statistically between age groups throughout the two fatigue tasks and recovery period.

Postactivation potentiation

Postactivation potentiation decreased to a similar extent in both age groups during the two fatigue tasks (main effect, $P < 0.01$; Fig. 6) despite a non significant tendency to a lesser potentiation in the elderly compared with young group, in concentric ($116.3 \pm 4.4\%$ vs $119.1 \pm 3.2\%$) and eccentric ($114.9 \pm 6.2\%$ vs $121.5 \pm 3.1\%$) in pre-fatigue condition. This decline occurred mainly after the first set of contractions and did not change during the following four sets of con-

tractions. For both groups, postactivation potentiation remained significantly depressed during the first 15 min of the recovery period for the concentric task before recovering to control values. The two groups of subjects exhibited a significant deficit in postactivation potentiation after 30 min of recovery following the eccentric task, with similar declines for the elderly ($17.1 \pm 4.4\%$ of control values) and young adults ($10.3 \pm 3.5\%$; $P > 0.05$).

Discussion

The current study appears to be the first to compare the neuromuscular fatigability of elderly and young adults during maximal concentric and eccentric contractions.

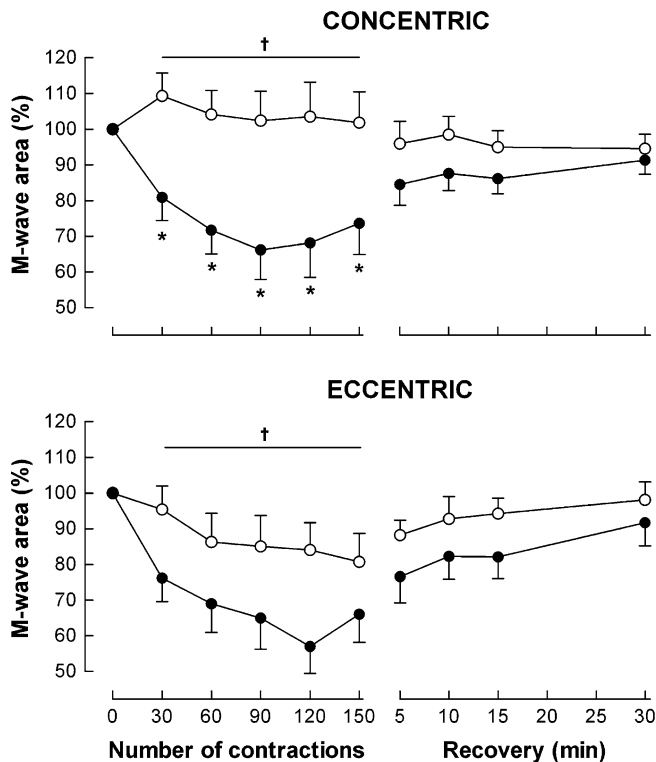


Fig. 5 Comparison of changes in M-wave area during the fatigue tests involving maximal concentric and eccentric contractions in young (*open circles*) and elderly (*filled circles*) groups. Data, expressed as percentage of initial values, are means \pm SE for 16 subjects in each group. Significant difference ($P < 0.05$): * between young and elderly adults; † with control values for elderly adults

The results show that the fatigability of the ankle dorsiflexor muscles during both types of contractions was greater in the elderly subjects, with no difference between the two sexes. In contrast to the young adults, who experienced greater fatigability during test involving concentric contractions compared with eccentric contractions, the elderly adults exhibited a similar decrease in torque for the two tasks. The results also suggest that the fatigue experienced by the two groups of subjects was mainly associated with peripheral alterations involving Ca^{2+} -controlled excitation-contraction coupling processes. In elderly adults, however, impaired neuromuscular propagation may have also contributed to the decline in force.

Task differences

To date, the neuromuscular fatigability of elderly adults has been mainly investigated during submaximal (Allman and Rice 2001; Bilodeau et al. 2001; Hunter et al. 2001; Kent-Braun et al. 2002) or maximal isometric contractions (Ditor and Hicks 2000; Lanza et al. 2004; Stackhouse et al. 2001). From these studies, it appears that the time to task failure is greater (Bilodeau et al. 2001; Hunter et al. 2004) or that the decline in MVC

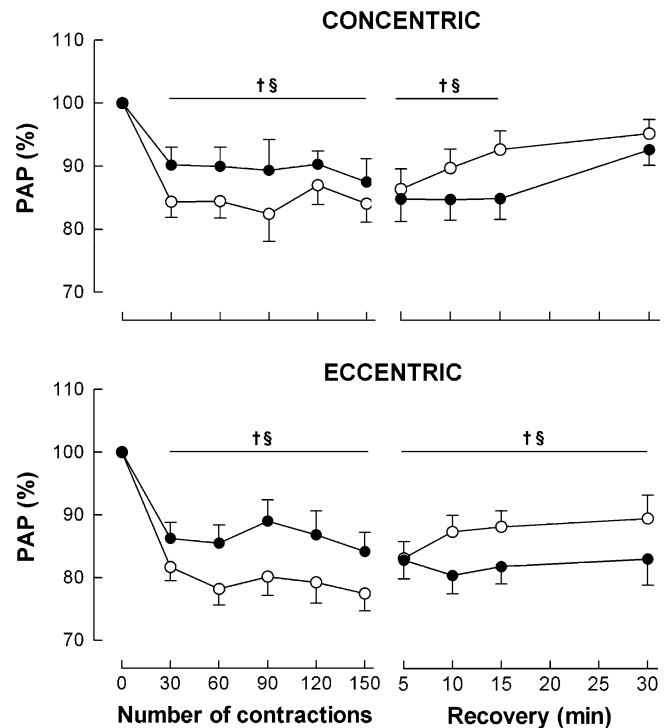


Fig. 6 Comparison of changes in postactivation potentiation (*PAP*) during fatigue tests involving maximal concentric and eccentric contractions in young (*open circles*) and elderly (*filled circles*) groups. Data, expressed as percentage of initial values, are means \pm SE for 16 subjects in each group. § and † denote significant difference ($P < 0.05$) with control values for young and elderly adults, respectively

torque is less (Kent-Braun et al. 2002; Lanza et al. 2004) or similar (Allman and Rice 2001; Stackhouse et al. 2001) for elderly adults compared with young adults. Despite the widely acknowledged task-dependent characteristics of fatigue (Enoka and Stuart 1992; Gandevia 2001), few studies have investigated the effect of dynamic contractions on the neuromuscular fatigability in elderly subjects. Among the studies that have examined these types of contractions, a similar degree of resistance to fatigue has been reported on the knee extensors of elderly and young adults (Laforest et al. 1990; Larsson and Karlsson 1978; Lindstrom et al. 1997). In contrast, others have found a greater resistance to fatigue in the ankle dorsiflexors of elderly adults (Lanza et al. 2004), but a greater fatigability of the knee extensors during repetitive concentric contractions for elderly adults (Petrella et al. 2005).

The current study found a greater susceptibility to fatigue for the ankle dorsiflexor muscles of elderly adults during maximal concentric and eccentric contractions. The discrepancy between our results and those of Lanza and colleagues (2004) for the concentric contractions may be explained by a greater duration of muscle activation during each effort in the current study. Our protocol involved both a lower speed of movement ($50^\circ/s$ compared with $90^\circ/s$ in the study of Lanza et al. 2004)

and initiation of the concentric and eccentric contractions from a preceding isometric MVC. The latter procedure allows more complete activation of the involved muscles during the course of the subsequent movement (Komi et al. 2000), which is not the case when voluntary activation leads directly to the onset of ankle movement (Lanza et al. 2004). Another possible explanation for this difference is that Lanza et al. (2004) performed concentric contractions over a 30° range centred about the midpoint of the full range of motion for each subject, whereas the current study used a standardised range of motion from 30 to 0° plantar flexion for all subjects.

Another new finding of the current study is that although fatigue was more pronounced during the concentric contractions in the young adults (Pasquet et al. 2000; Tesch et al. 1990), there was no difference in the loss of force between the two contraction types in the elderly adults. This greater torque decline in the elderly compared with young subjects is difficult to explain on the basis of the current results, but could be related to the greater shortening of the twitch CT during the course of the eccentric contractions, and thereby to a reduced interaction time between the contractile proteins (see below). Further investigations are, however, needed to clarify the exact mechanism.

Central and peripheral mechanisms

Various studies have shown that elderly adults are capable of achieving the same level of voluntary activation as young adults during isometric MVC (Allman and Rice 2001; Kent-Braun et al. 2002; Lanza et al. 2004), and dynamic (concentric and eccentric) maximal contractions at different speeds (Klass et al. 2005). In agreement with some previous studies using different types of fatiguing tasks (Allman and Rice 2001; Lanza et al. 2004), the current study did not detect any significant change in voluntary activation during isometric MVCs performed after each set of 30 contractions either in the young or elderly adults. It may be argued that because voluntary activation was tested 20 s after each set of contractions, central fatigue may have already recovered at that time and that the absence of voluntary activation failure during an isometric MVC does not mean that none occurred during the dynamic contractions (Cheng and Rice, 2005). However, the ratio of voluntary aEMG, recorded during the last five concentric or eccentric contractions of each set, to M-wave amplitude elicited immediately after the last contraction, was not significantly modified during the two fatiguing tasks in either age group. This ratio, which control for fatigue-related changes of the muscle fibre membrane, also provides an estimate of the neural adjustments (Klass et al. 2005). Therefore, in agreement with other studies using the dorsiflexor muscles (Kent-Braun et al. 2002; Lanza et al. 2004), our results suggest that voluntary activation was optimal during the two fatigue tasks and that central fatigue did not play a major role in

the force decrease during repeated maximal concentric and eccentric contractions performed at slow velocity.

Although the M-wave amplitude and area did not change significantly during the two fatigue protocols for the young adults, they decreased progressively during both fatigue tasks for the elderly adults. The absence of decline in M-wave amplitude, which is often observed during intermittent isometric contractions (Duchateau and Hainaut 1985) or repetitive isokinetic movements (Pasquet et al. 2000) in young subjects, suggests that a brief rest period between each muscle contraction was sufficient to maintain sarcolemmal excitability and neuromuscular propagation at a normal level. The significant reduction in M-wave amplitude and area for the elderly adults, however, contrasts with the study of Lanza et al. (2004) showing no change after repeated concentric contractions in the tibialis anterior muscle and could again be explained by a greater duration of muscle activation during each contraction in the current study (see above). The decrease in M-wave area without a change in its duration suggests potential alterations in sarcolemmal excitability or neuromuscular propagation (Ditor and Hicks 2000; Duchateau and Hainaut 1985). Consistent with this interpretation, Cupido et al. (1992) suggested an age-related change in the ability of the Na⁺/K⁺-ATPase to cope with the ionic perturbations associated with muscle activity. Collectively, the results indicate that the greater fatigability exhibited by the elderly adults may have been partially due to a fatigue-related reduction in peripheral excitation.

Changes in excitation–contraction coupling intensity, which is closely controlled by intracellular movement of Ca²⁺ and myosin light-chain phosphorylation, can be indirectly studied in humans by comparing the M-wave and mechanical twitch. Although the time course of the twitch is related to phasic movement of cytosolic Ca²⁺ during a contraction (Duchateau and Hainaut 1986b; Hainaut and Desmedt 1974), changes in postactivation potentiation during fatigue appears to be more closely controlled by myofibrillar Ca²⁺ sensitivity (Grange and Houston 1991; Sweny et al. 1993). The current results indicated that P_t increased after the first set of contractions in both fatigue protocols for young adults before declining progressively during the remainder of the task. The extent of P_t enhancement, however, was greater during the eccentric contractions, which may be attributable to variable contributions of potentiation and fatigue to the resulting muscle force during the course of the task (Garner et al. 1989; Pasquet et al. 2000). Because the potentiating capacity of a muscle does not differ between concentric and eccentric contractions in non fatigue condition (Baudry and Duchateau 2004), the lower P_t augmentation observed during the concentric contractions was probably related to a more intense level of fatigue caused by greater energetic cost (Barclay et al. 1993; Constable et al. 1997) or greater metabolites accumulation (Carrasco et al. 1999; Westerblad and Allen 1995) compared with eccentric contractions. In contrast, P_t was depressed to a similar

extent during the two fatigue tasks from the first set of contractions to the end of the task in the elderly adults. Therefore, the age-related difference in fatigability was caused by a more pronounced alteration in excitation-contraction coupling. Because PAP is similarly depressed during the concentric and eccentric fatiguing tasks in both age groups, impairment in calcium kinetics should explain the greater decline of P_t in the elderly adults.

In the current study, the maximal rate of twitch torque development ($+dP_t/dt$) and relaxation ($-dP_t/dt$) changed in the same way as P_t amplitude during the course of the two fatigue tasks. Whereas, $+dP_t/dt$ and $-dP_t/dt$ increased after the first set of contractions in both fatigue tasks for young adults before declining progressively during the remainder of the task, both parameters decreased immediately from the beginning of both tasks and to a greater extent in elderly adults. Therefore, the data indicate that the muscle contractile kinetics are slowed down during both fatiguing contractions and to a greater extent in the elderly compared with young adults. In both age groups, however, the reduced torque was associated with a shortening of the twitch CT after the two fatiguing tasks and $TR_{1/2}$ after eccentric contractions. Such shortening of the twitch time course during fatigue is surprising and contrasts with the usual slowing of the twitch reported after sustained isometric contractions (Allman and Rice 2001; Duchateau and Hainaut 1985; Lanza et al. 2004). However, other fatigue studies using intermittent contractions also showed a shortening of the twitch time course (Klass et al. 2004; Pasquet et al. 2000; Vollestad et al. 1997; Millet et al. 2001). This opposite change in the speed-related parameters is difficult to explain on the basis of the present experimental results. However, they suggest that $+dP_t/dt$ and CT, as well as $-dP_t/dt$ and $TR_{1/2}$ do not measure exactly the same parameters. For example, it has been suggested that $+dP_t/dt$ is more closely associated with the intensity of Ca^{2+} release, whereas CT is more related to the amount of Ca^{2+} release and duration of the actin-myosin interaction (Duchateau and Hainaut 1986a, b).

Under our experimental conditions, several intracellular processes may have interacted to decrease muscle force in different ways in the two fatigue tasks and in both age groups. The observation that a deficit in P_t was still present after a 30 min of recovery excludes the role of metabolites at this stage (Jones 1996; Westerblad et al. 1991), but again suggests a possible impairment of excitation-contraction coupling as a key factor in twitch torque reduction in both age groups. This interpretation is consistent with the findings that P_t was still substantially depressed (low-frequency fatigue; see Jones 1996) at a time when the M-wave had nearly recovered its initial values in both fatigue protocols. For the concentric task, the reduction of P_t may be explained by an impaired Ca^{2+} release because postactivation potentiation had returned to its control values at this time, suggesting that the myofibrillar sensitivity for Ca^{2+} has

already recovered. Thirty minutes after the end of the eccentric task, however, P_t , $TR_{1/2}$ and postactivation potentiation were still depressed indicating an impairment of Ca^{2+} release and reuptake by the sarcoplasmic reticulum, and alteration in the myofibrillar sensitivity for Ca^{2+} .

In conclusion, the present study shows that the fatigability of the ankle dorsiflexor muscles during repeated maximal concentric and eccentric contractions was greater in elderly adults. Unlike the young adults who displayed a greater fatigability during the concentric task, the elderly adults exhibited a comparable decrease in torque in both contraction types. The results further indicate that, in both age groups and fatigue tasks, these differences were not related to central fatigue, but instead to peripheral mechanisms that involved Ca^{2+} -controlled excitation-contraction coupling. The fatigue experienced by the elderly adults, furthermore, may have been amplified by an impairment of neuromuscular propagation.

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