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Power loss is greater in old men than young men during fast plantar flexion contractions

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Dalton BH, Power GA, Vandervoort AA, Rice CL. Power loss is greater in old men than young men during fast plantar flexion contractions. *J Appl Physiol* 109: 1441–1447, 2010. First published September 9, 2010; doi:10.1152/jappphysiol.00335.2010.—It is unclear during human aging whether healthy older adults (>70 yr old) experience greater, lesser, or the same fatigability compared with younger adults. The reported disparate findings may be related to the task-dependent nature of fatigue and the limited number of studies exploring nonisometric contractile function and aging. The purpose here was to determine the effects of fast shortening contractions on the fatigability of the triceps surae in 10 young (~24 yr old) and 10 old (~78 yr old) men using isometric and dynamic measures. Participants performed 50 maximal velocity-dependent plantar flexions at a constant load of 20% maximal voluntary isometric contraction (MVC). Isometric twitch properties and MVCs were tested at baseline and during and following the fatigue task. Voluntary activation was similar between the old and young (~98%) and was unaltered with fatigue. The old had 26% lower ($P < 0.01$) isometric MVC torque and 18% slower ($P < 0.01$) maximal shortening velocity than the young. Hence, peak power was 38% lower in the old ($P < 0.01$). At task termination, MVC torque was maintained in the old ($P = 0.15$) but decreased by 21% in the young ($P < 0.01$). Twitch half-relaxation time was lengthened in the old at task termination by 26% ($P < 0.01$) but unchanged in the young ($P = 0.10$). Peak power was reduced by 24% and 17% at task termination in the old and young, respectively ($P < 0.01$). Despite a better maintenance in isometric MVC torque production, the weaker and slower contracting triceps surae of the old was more fatigable than the young during fast dynamic efforts with an unconstrained velocity.

shortening velocity; aging; isometric strength; fatigue; soleus

SARCOPENIA is the age-related loss of muscle mass accompanied by various functional alterations within the neuromuscular system (1, 31). Together these changes contribute to reductions in muscle strength and slower contractile kinetics, resulting in a leftward shift in the torque-velocity (37) and torque-frequency (3) relationships. The combined effect of strength loss and contractile slowing creates even greater reductions in muscle power than the decreases in either variable alone (29, 36). During voluntary isometric contractions, the leftward shift in the torque-frequency curve may allow a given relative torque output to be achieved with lower motor unit (MU) discharge rates from the active MU pool, although it is unclear whether MU recruitment thresholds are altered with age (5, 15, 22). Such changes may however be advantageous for older

adults, at least during high-intensity isometric contractions, which require less ATP turnover to support the lower MU discharge rates for a given contraction level, and hence minimize fatigue (24). Thus it has been reported that for sustained isometric contractions older adults are less fatigable than young adults (24), but during dynamic contractions older individuals can experience more (6, 29, 33), less (27), or the same (7) fatigue compared with younger adults. The inconsistencies in the literature on dynamic function may be related to the age of the participants, muscle group tested, type of task, or the criterion measure used to assess fatigue. Because dynamic contractions include a velocity component, declines in isometric contractile speed (13) and voluntary shortening velocity (29) may be disadvantageous to muscles in older adults during these tasks. Thus further studies are needed to explore the impact of reductions in both strength and shortening velocity on dynamic muscle function and fatigability during repetitive tasks in old compared with young adults.

Recently, it has been reported that old men are more fatigable than young men when performing velocity-dependent shortening contractions of the knee extensors (33) and dorsiflexors (29). These dynamic actions are characterized by the participant contracting as fast as possible against a preset load, whereby velocity is unconstrained by the testing device and speed of movement is determined by the ability of participants to contract maximally through a predetermined range of motion (8, 9, 29). This is different from some other studies that have used slow to moderate speed isovelocity tasks (6, 7, 27) during which the velocity is constrained by the testing device and the load is variable and highly dependent on subject effort. The results from isovelocity studies are contradictory and hard to reconcile and may relate to the different contraction speeds used in the tasks, or muscle group tested. Velocity-dependent contractions allow the component of velocity to be assessed, which may be especially important in aged subjects in which isometric speed of contraction (13) and dynamic velocity (29, 37) are known to be compromised. A limitation of the relatively few studies that have focused on velocity-dependent contractions is that isometric muscle capacity was not tested during or following the fatigue task. Because independent mechanisms are responsible for reductions in either isometric torque or shortening velocity (2), an important aspect of the present study was to elucidate potential neuromuscular factors related to the impairment of older adults to perform velocity-dependent tasks when tested by voluntary shortening velocity, voluntary and evoked isometric contractile properties, and neuromuscular activation through surface electromyography (EMG) and voluntary activation.

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Unlike most other limb muscles during the adult aging process, the soleus is well maintained into the eighth decade of life with respect to the number of MUs (14), maximal sustained MU discharge rates (13), and muscle mass (17, 30). Because of the homogeneous muscle fiber composition (>80% slow twitch) of the soleus compared with other limb muscles (23, 39) and the greater preservation of its MU function and morphology, this model allows for the exploitation of age-related impairments in muscle shortening velocity on fatigability to be evaluated with limited influence from MU remodeling (13, 14, 30). Although the soleus is not the only plantar flexor it is by far the largest contributor to plantar flexor torque contributing nearly 70% of triceps surae torque in the extended knee position (18). When the knee is flexed to $\sim 90^\circ$, as in the present study, the contribution of the gastrocnemii, the other large contributor to plantar flexion torque, is reduced by $\sim 23\%$ (11), thus requiring an even greater contribution by the soleus in this position. The purpose here was to use the plantar flexion model, with a strong dependence on the uniqueness of the soleus with regard to its histophysiology and its apparent relatively well-preserved neuromuscular properties in response to aging, to assess changes in isometric and dynamic shortening function following plantar flexion fatigue in old and young men. Fatigue was induced by 50 repetitive dynamic shortening contractions performed as fast as possible with a moderate load. We hypothesized that due mainly to greater impairments in contractile shortening function rather than reduced torque-generating capacity that the old men would have greater power loss following fatigue than the young men.

MATERIALS AND METHODS

Participants. Ten old men (age 77.5 ± 3.0 yr, height 175.5 ± 7.9 cm, body mass 88.6 ± 13.1 kg) and ten young men (age 24.1 ± 2.8 yr, height 175.0 ± 8.7 cm, body mass 78.6 ± 7.9 kg) volunteered for this study. To eliminate sex differences as a covariate in the muscle fatigue response (19), we only tested men in this study. The old men were recruited from local exercise groups, while the young men were recruited from the university environment. All men were recreationally active and healthy with no evidence of neuromuscular disease. The local university's ethics review board for experimentation on humans approved the study, and oral and written informed consent was obtained from each participant before experimental testing.

Experimental arrangement. Data were collected for the dynamic fatigue task during one visit to the neuromuscular laboratory. A Biodex System 3 multijoint dynamometer was used to record plantar flexion torque, ankle position, and velocity in either the isometric or the isotonic mode. Because of the inherent mechanical limitations of the dynamometer, these contractions are not strictly isotonic nor are they isoinertial as the load is fixed mechanically and not influenced by gravity. Participants were seated comfortably in a reclined position with the hip joint at 90° , and to minimize contributions of the gastrocnemii to plantar flexor torque (11) the knee angle was set at 90° . The ankle angle was set at 10° of dorsiflexion (0° = neutral) for all isometric contractions and for the beginning of the dynamic shortening (velocity dependent) contractions. All tests were performed on the right (dominant) leg. Two Velcro straps across the toes and dorsum of the foot and a custom-made binding at the ankle secured the foot to the footplate. During all contractions, the participants were fastened securely to the seat of the Biodex with inelastic straps around the shoulders and waist. A thigh support with an inelastic strap was used for stabilization of the limb and to minimize involvement of the thigh muscles. The ankle joint was aligned with the axis of rotation of the dynamometer. All plantar flexor torques,

velocities, and positions were sampled at 100 Hz using a 12-bit analog-to-digital converter (Power 1401; Cambridge Electronic Design, Cambridge, UK) and digitized online using Spike2 software (Cambridge Electronic Design).

Surface EMG signals were recorded from the soleus, medial gastrocnemius, and tibialis anterior using self-adhering surface pediatric cloth electrodes (H59P Repositionable Monitoring Electrodes; Kendall, Mansfield, MA). The skin was cleaned aggressively with alcohol before electrode placement. Using a 2-cm interelectrode distance, one electrode pair was positioned over the medial gastrocnemius muscle belly, a second pair ~ 2 cm below the gastrocnemii border, along the longitudinal axis over the soleus, and a third pair along the longitudinal axis of the tibialis anterior (7 cm distal to the tibial tuberosity and 2 cm lateral to the tibial anterior border). Two ground electrodes were placed over the right patella (one for the plantar flexor EMG channels and the other for the dorsiflexor EMG channel). Surface EMG signals were preamplified ($\times 100$), amplified ($\times 2$), bandwidth filtered (10 Hz to 1 kHz), converted by a 12-bit analog-to-digital converter (Power 1401, Cambridge Electronic Design), and sampled online at 2,000 Hz.

Electrically evoked twitches and compound muscle action potentials (M-waves) were elicited from the plantar flexors using a bar electrode held in the distal portion of the popliteal fossa between the origins of the heads of the gastrocnemius to stimulate the tibial nerve. Single stimuli were generated via a 100- μ s square-wave pulse set at a maximal voltage of 400 V (Digitimer stimulator, model DS7AH; Digitimer, Welwyn Garden City, UK).

Experimental procedures. Range of motion of the ankle was set at 25° , from 10° dorsiflexion to 15° plantar flexion (end of dynamic contraction). To elicit the maximum M-wave and the corresponding twitch, the current was increased gradually until a plateau was achieved in the M-wave peak-to-peak amplitude and in the peak twitch torque. The current was then increased by 10–15% to ensure supramaximal stimulation (average dial setting of 378 ± 92 mA) throughout the protocol. Nonactivation of antagonist muscles was ensured by visual inspection and palpation. Participants then performed three to five ~ 7 -s maximal isometric voluntary contractions (MVCs). Extra isometric MVCs were performed if the first three attempts varied in peak torque by $>5\%$. Each attempt was preceded (~ 2 s) by a supramaximal twitch delivered at rest, another delivered during the peak plateau of MVC torque (T_s) and another ~ 2 s following (T_r) when the plantar flexors were relaxed fully. Participants were encouraged strongly during all maximal voluntary attempts and were provided visual feedback on a computer monitor. All isometric MVCs were separated by at least 2 min of rest.

Following the completion of the isometric MVCs, participants were familiarized with the maximal effort velocity-dependent shortening contractions. These contractions are characterized by a constant load, and an unconstrained velocity dependent on how fast the participant can voluntarily move this load through a range of motion. Participants performed dynamic plantar flexion contractions through the 25° range of motion with a load set to 20% MVC. Upon contracting through the range of motion, the participant relaxed and the dynamometer returned the foot back to its starting position for subsequent or repetitive contractions. For familiarization, the participants performed several velocity-dependent shortening contractions each separated by short rest intervals (~ 5 – 10 s). To ensure a maximal effort (peak velocity), all participants were instructed to move the load "as fast as possible through the entire range of motion" and exhorted while performing each contraction. Participants were given visual feedback of the velocity profile produced on a computer monitor. Once consistent peak velocity was achieved (no change during 5 consecutive attempts), the participants performed five consecutive contractions (to mimic the fatigue task) for a total of ~ 10 – 15 dynamic contractions. Familiarization was followed by 10 min of rest to ensure no residual fatigue was present. Finally, the participants performed the fatigue task, which consisted of 50 maximal effort velocity-dependent short-

ening contractions at a load of 20% MVC. To move this load repetitively through the full range of motion for 50 contractions translates into a moderate resistance. Indeed, from pilot testing it was found that loads beyond 50% of isometric MVC could not be successfully maintained for more than a few contractions without range of motion failure in most subjects. The duration of each contraction throughout the fatigue protocol was ~1.4 s for the old men and ~0.9 s for the young (i.e., to include the contraction time and the time needed for the footplate to return to the starting position). Approximately 5 s following the 25th and 50th dynamic contractions an isometric MVC and corresponding evoked measures were performed. The isometric testing procedures lasted ~15 s.

Data analysis and statistics. Although there can be some possible inherent limitations of surface EMG recordings during dynamic contractions that should be recognized (16), surface EMG nevertheless can provide a useful relative value of neuromuscular activation. To analyze surface EMG data of the soleus, medial gastrocnemius, and tibialis anterior, the root mean square (RMS) value was calculated over a 1-s interval about the peak torque for all isometric MVCs and normalized to the RMS of the baseline MVC. To compare the surface EMG signal values for the dynamic contractions during the fatigue protocol, a RMS value was calculated over the full range of motion of each shortening contraction and averaged over every five contractions. This value was then normalized to the averaged RMS EMG from the first five dynamic contractions of the fatigue task.

To provide an indication of sarcolemmal excitability and conduction velocity, peak-to-peak amplitude, duration, and area (the area under the negative and positive peaks) of the soleus M-wave were analyzed. Inherent changes in the contractile function of the plantar flexors were assessed by measures of peak twitch torque (N·m), time to peak twitch torque (TPT; ms), and half-relaxation time (HRT; ms) of the twitch. The post-MVC isometric twitch torque was used to assess voluntary activation of the plantar flexors via the interpolated twitch technique [%activation = $[1 - (T_e/T_r)] \times 100$] (38).

The maximum torque of the isometric MVC attempts was taken as the baseline value. For the dynamic contractions, baseline velocity and power were taken from the maximum value during the fatigue protocol, which occurred within the first five contractions of the task. Peak power was calculated as the product of the external load (N·m) and maximal shortening velocity (rad/s). For analysis of the fatigue task, velocity and power of each dynamic contraction were normalized to the baseline value and an average was calculated over every five contractions.

Data were analyzed using SPSS version 16 (SPSS, Chicago, IL). Unpaired *t*-tests were used to compare all baseline values, and range of motion of the fatigue task between age groups, except for voluntary activation in which a Mann-Whitney *U*-test was used to analyze group differences. A two-way analysis of variance (age \times time) with repeated measures was used to analyze all normalized data for the fatigue protocol. The level of significance was set at $P < 0.05$. Post hoc analysis using unpaired *t*-tests was performed with a Bonferroni correction factor to determine differences when significant main effects or interactions were present. Effect sizes (ES) were calculated using the partial eta-squared method to explore the strength of apparent statistical effects, and 95% confidence intervals for the differences in means were calculated, as appropriate. A Pearson correlation coefficient (*r*) and a linear regression analysis (R^2) were performed to evaluate the relationship and shared variance between HRT and peak shortening velocity throughout the fatigue task. Descriptive statistics reported in the text and table are reported as means \pm standard deviations (SD), whereas all data reported in the figures are means \pm standard errors of the mean (SE).

RESULTS

Baseline. Compared with the young men, the old men were 26% weaker for isometric plantar flexion MVC torque ($P <$

0.01, ES = 0.37) but were equally capable of high voluntary activation (~98%; $P = 0.39$; Table 1). For peak shortening velocity the old men were 18% slower than the young ($P < 0.01$, ES = 0.42, Table 1). When peak power, the product of torque and velocity, was compared the old men exhibited 38% less power than the young men ($P < 0.01$, ES = 0.46; Table 1). Evoked peak twitch torque tended to be 15% lower in the old men compared with the young ($P = 0.08$, ES = 0.16; Table 1). Twitch TPT was 21% longer ($P < 0.01$, ES = 0.44) and HRT was 13% longer ($P < 0.05$, ES = 0.28), in the old men than the young (Table 1). The old men had a ~47% smaller peak-to-peak amplitude of the soleus M-wave than the young ($P < 0.05$, ES = 0.25; Table 1) with no differences in M-wave area ($P = 0.76$) or duration ($P = 0.60$).

Fatigue task. Range of motion remained constant for all participants throughout the fatigue protocol and was not different between age groups ($P = 0.65$). For peak power, there were main effects for time ($P < 0.01$, ES = 0.73) and age ($P < 0.01$, ES = 0.46), and thus for both age groups, peak power was reduced from baseline for contractions 36–50 of the fatigue task compared with all contractions before and including the 20th. The old men exhibited greater reductions in peak power than the young men for contractions 16–25 and 31–50 (Figs. 1 and 2).

Isometric fatigue measures. For isometric MVC torque, there was a significant main effect for time ($P < 0.01$, ES = 0.54) and age ($P < 0.05$, ES = 0.31) and an interaction ($P < 0.05$, ES = 0.26) as a result of the fatigue protocol. The isometric MVC torque was unaltered from baseline following termination of the fatigue task for the old men but was decreased by 20% at task termination for the young (Figs. 1 and 2). However, this age-related difference in isometric MVC torque was not due to voluntary activation failure as both age groups were capable of high activation throughout the fatigue protocol (range: 95–98%). Unlike MVC torque, evoked peak twitch torque was increased similarly to $118.4 \pm 17.5\%$ in both age groups by the end of the fatigue task as there was only a main effect for time ($P < 0.01$, ES = 0.40, Fig. 3A).

Table 1. Baseline neuromuscular characteristics of the triceps surae

	Group (n = 10)		95% CI
	Young	Old	
Maximum voluntary isometric contraction, N·m	190.8 \pm 28.0	141.1 \pm 39.7*	-82.1, -17.5
Voluntary activation, %	98.3 \pm 2.9	97.1 \pm 4.8	-5.0, 2.5
Peak shortening velocity, rad/s	5.2 \pm 0.5	4.3 \pm 0.7*	-1.5, -0.4
Peak power, W	198.4 \pm 37.8	122.2 \pm 49.2*	-117.5, -35.1
Peak twitch torque, N·m	24.0 \pm 4.1	20.3 \pm 4.9†	-7.9, 0.6
Time to peak twitch, ms	135.6 \pm 24.9	170.9 \pm 16.0*	14.7, 55.8
Half-relaxation time, ms	103.9 \pm 14.7	119.3 \pm 10.9*	3.2, 27.5
M-wave peak-to-peak amplitude, mV	9.8 \pm 5.3	5.2 \pm 2.6*	-8.8, -0.4

Values are means \pm SD with 95% confidence intervals (CIs) for the difference in means. The old men were weaker, slower, less powerful, and had lower M-wave peak-to-peak amplitudes than the young (* $P < 0.05$). Peak twitch torque tended to be lower in the old men than the young († $P < 0.08$). Peak shortening velocity and peak power were determined using a load of 20% isometric maximum voluntary contraction.

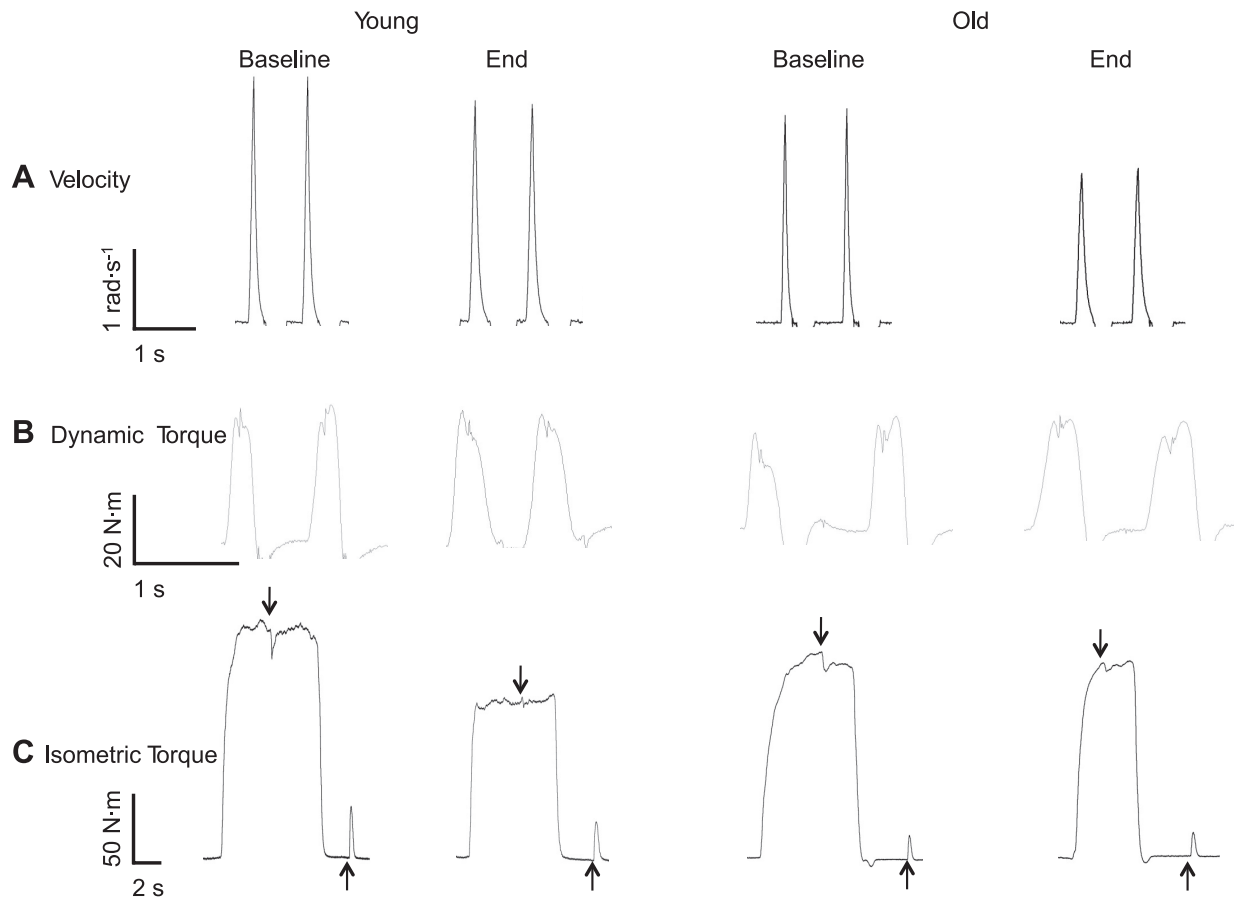


Fig. 1. Representative torque and velocity data sample from an old and young subject at baseline and following task termination (End). *A*: velocity tracings of the maximum effort shortening contractions. *B*: torque tracings of the maximum effort shortening contractions. *C*: torque tracings of the isometric MVC and corresponding superimposed twitch (T_s) and posttwitch (T_r) responses, which were used to calculate voluntary activation. The vertical arrow indicates where the pulse was given.

For TPT there was only a time effect ($P < 0.05$, $ES = 0.24$), meaning that TPT decreased similarly to $89.4 \pm 13.4\%$ following task termination for both age groups. However, for HRT there was a main effect for time ($P < 0.01$, $ES = 0.35$) and age ($P < 0.05$, $ES = 0.39$) and an interaction ($P < 0.05$, $ES = 0.25$). Twitch HRT was slowed by 21% at the middle

and even further lengthened by 26% following task termination compared with baseline for the old men, but HRT was unaltered throughout the task for the young men (Fig. 3B). Furthermore, there was a moderate correlation ($r = -0.54$, $P < 0.01$) between HRT and peak shortening velocity with a significant linear regression [velocity (in rad/s) =

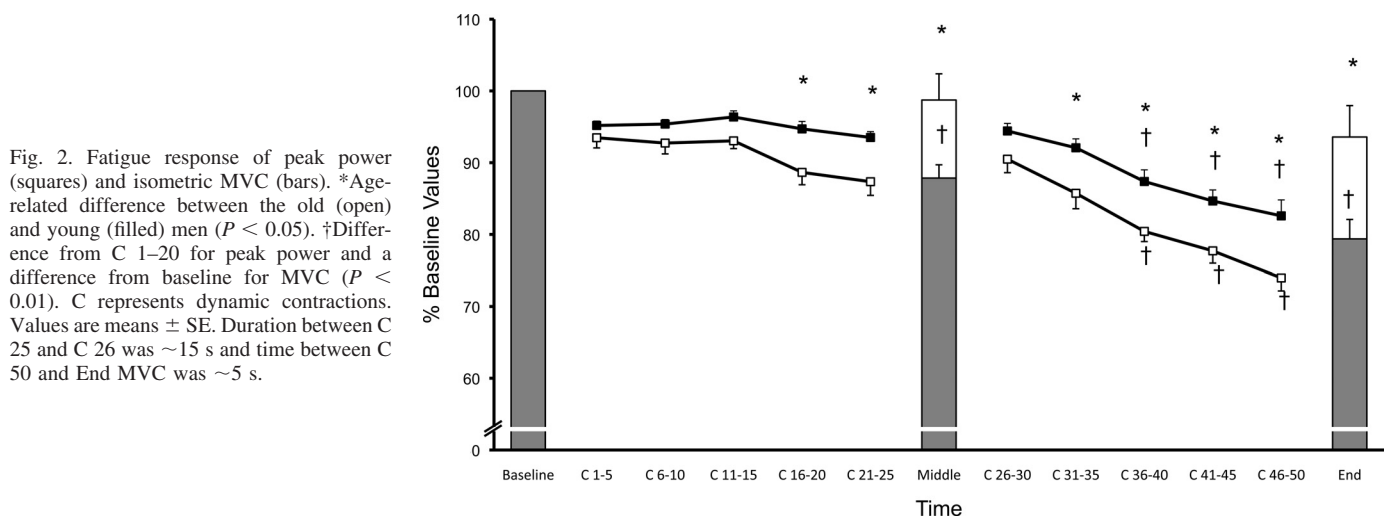


Fig. 2. Fatigue response of peak power (squares) and isometric MVC (bars). *Age-related difference between the old (open) and young (filled) men ($P < 0.05$). †Difference from C 1–20 for peak power and a difference from baseline for MVC ($P < 0.01$). C represents dynamic contractions. Values are means \pm SE. Duration between C 25 and C 26 was ~ 15 s and time between C 50 and End MVC was ~ 5 s.

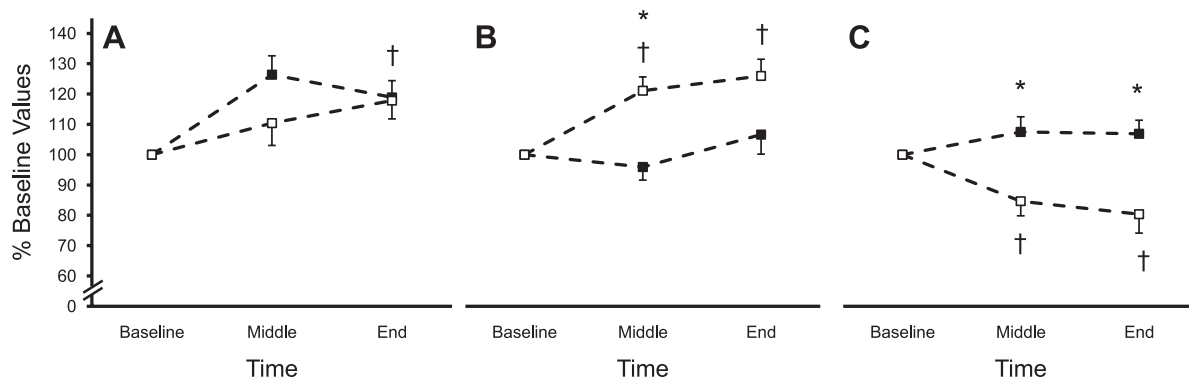


Fig. 3. Fatigue response of isometric peak twitch torque (A), twitch half-relaxation time (B), and M-wave peak-to-peak amplitude (C). Dashed line indicates the performance of the fatigue task. *Age-related difference between the old (open) and young (filled) men ($P < 0.05$). †Difference from baseline ($P < 0.01$). Values are means \pm SE.

$-0.019 \cdot \text{half-relaxation time (in ms)} + 6.58$, $R^2 = 0.29$, $P < 0.01$].

Electromyographic fatigue measures. For peak-to-peak amplitude of the soleus M-wave there was a main effect for age ($P < 0.01$, ES = 0.41) and an interaction ($P < 0.01$, ES = 0.37) with the old men having a reduction of 20% peak-to-peak amplitude by task termination. Because there were no fatigue-related changes in M-wave peak-to-peak amplitude for the young, the old men exhibited $\sim 23\%$ lower values than the young throughout (Fig. 3C). For M-wave area, there was an age effect ($P < 0.01$, ES = 0.45) and an interaction ($P < 0.01$, ES = 0.35), meaning that the old men had 24% and 26% lower values at the middle (old: $87.9 \pm 12.3\%$; young: $116.2 \pm 18.9\%$) and following the fatigue task (old: $87.1 \pm 19.9\%$; young: 117.0 ± 20.7) compared with the young, respectively. However, for M-wave duration there were no fatigue-related differences.

For both the soleus and medial gastrocnemius EMG during the isometric MVCs, there was only a main effect for time ($P < 0.01$, soleus ES = 0.33, medial gastrocnemius ES = 0.18). Soleus and medial gastrocnemius RMS amplitude of the MVC EMG was reduced similarly to $86.4 \pm 16.6\%$ and $85.6 \pm 22.3\%$, respectively, following the task for both age groups. However, for the tibialis anterior, the RMS amplitude was similar between the old and young men and was unaltered by the fatigue task. During the dynamic contractions there was only a time effect ($P < 0.01$, soleus ES = 0.50, medial gastrocnemius ES = 0.34) for both the soleus and medial gastrocnemius. The RMS amplitude of the dynamic contractions was reduced to $85.5 \pm 14.3\%$ and $83.8 \pm 21.7\%$ for the soleus and medial gastrocnemius, respectively, by the end of the fatigue task for both age groups with no differences for the tibialis anterior (range: $90.4 \pm 19.5\%$ to $103.7 \pm 23.1\%$).

DISCUSSION

This study investigated the age-related fatigability of the triceps surae (primarily the soleus) in old and young men comparing measures of both isometric and dynamic properties during and following a repetitive velocity-dependent plantar flexion task. In accordance with our hypothesis, the slower, weaker, and less powerful old men were more fatigable than the young when peak shortening velocity, and hence peak power, was used as the criterion fatigue measure. Following

the fatigue task, peak power was reduced by 26% for the old men, whereas the young men maintained their peak power to a greater extent with only a 17% reduction. However, for the measure of isometric MVC torque, the outcome was reversed. The isometric MVC torque was unaltered in the old men but was reduced by 21% in the young. Voluntary activation and RMS amplitude of the surface EMG did not differ between age groups during and following the fatigue task; thus the main sites of fatigue likely were peripheral in nature. Because the old had a smaller M-wave peak-to-peak amplitude and subsequently smaller M-wave area and greater slowing of contractile properties (i.e., HRT) by the end of the fatigue task compared with the young men, the ability of the old men to maintain dynamic performance may have been hindered by the muscle's inability to relax and contract quickly and possibly impaired sarcolemmal excitability. By evaluating isometric MVC during and following the fatigue task we were able to eliminate torque-generating capacity per se as a potential factor responsible for greater fatigability in the old men compared with the young. Thus the triceps surae of older adults is more fatigable than for young men during a fast unconstrained velocity task, suggesting impairments related to shortening velocity are important determinants in age-related fatigability.

Baseline. Our results corroborate that plantar flexor isometric MVC torque is 26% less and peak twitch torque is 15% less in the old men compared with the young (13, 35, 40). However, the ability to produce a maximum isometric voluntary effort, as assessed by the interpolated twitch technique, was not a limitation for either age group when participants are well practiced with the task (13, 21, 35). Also, similar to previous studies on the plantar flexors (13, 34, 40), the old men exhibited slower evoked isometric contractile properties and a $\sim 47\%$ smaller soleus peak-to-peak M-wave amplitude than the young. Here we also report that dynamic peak shortening velocity of the plantar flexors was 18% slower in the old men (Table 1). Because peak power is the product of torque and shortening velocity, the old men produced 38% less peak power than the young, which is similar to results reported from previous studies for this (37) and other muscle groups (29). With a similarity between the old and young men in maximum MU discharge rates [in the soleus (13)], and for voluntary activation of the plantar flexors in this study, the age-related impairments in torque production, evoked and voluntary contractile speed,

and power seem to be related to structural and functional alterations at the peripheral level (20, 30, 37, 42).

Fatigue. Our study, which utilized an unconstrained velocity to allow movement to vary freely with a constant load, determined that the old men had a greater reduction in power than the young and this was mainly due to fatigue-induced impairments in shortening velocity. These results are similar to the few previous studies on other muscles using this type of task (29, 33). In addition to testing dynamic muscle function after the dynamic fatigue task we also tested isometric muscle function. This was not performed in the previous studies following this type of fatigue task, but is an important assessment to help understand the interplay of the various factors that could affect fatigue. In two studies on aging and dynamic fatigue it was found that following a slow (0.87 rad/s) dorsiflexion and a moderate-speed (2.09 rad/s) knee extension isovelocity task the reduction in isometric MVC torque was not different between the young and old subjects (6, 7). In our study following fast (i.e., 4–5 rad/s) unconstrained dynamic contractions, isometric MVC torque was maintained to a better extent in the old men than the young. Although these studies are not directly comparable due to the fatigue task differences they do support that torque-generating capacity per se is not a key factor in the greater loss of power for the old men compared with the young.

In agreement with a previous report in the dorsiflexors (29), the greater fatigue of power in the old was not due to a larger decrease in neuromuscular activation of the agonists or increase in antagonist coactivity compared with the young men. For both age groups, the soleus and medial gastrocnemius RMS amplitudes from the dynamic contractions were reduced similarly by 14 and 16%, respectively, and the tibialis anterior RMS amplitude did not change. Furthermore, both age groups were capable of high and similar isometric voluntary activation (>95%) at the end of the dynamic fatigue task. This maintained high isometric voluntary activation following velocity-dependent fatigue has been reported previously for only young subjects in various muscle groups (8, 9), but similar to those testing voluntary activation following an isovelocity task (6, 7, 27). These measures combined suggest that factors related to voluntary activation were not different and cannot help explain the greater dynamic fatigability in the old men compared with the young.

Previous studies have reported that following an isometric fatigue task, isometric torque loss is equal to (4) or better preserved (7, 12, 27) in old than young adults. These seem to be consistent findings across the literature and none have reported greater fatigability in old compared with young for isometric tasks. Despite our finding that the old men were more fatigable than the young, which agrees with the two other studies (29, 33) using velocity-dependent contractions in other muscle groups, studies that have used constrained velocity (isovelocity) during dynamic contractions have reported variable results for power loss. For the dorsiflexors at a moderate velocity (1.57 rad/s) old men were found to be less fatigable (27), whereas at a slow velocity (0.87 rad/s) old men were more fatigable than their young counterparts (6), and for the knee extensors at a faster velocity (2.09 rad/s) equal fatigue was reported in both age groups (7). On the surface, these disparate results are not easily explained but are likely related to the different durations of the isovelocity tasks and the different slow to moderate speeds in the various muscle groups. Thus

they are not helpful in explaining our findings using relatively fast (old: 4.3 ± 0.7 rad/s, young: 5.2 ± 0.5 rad/s) and unconstrained velocities of contraction.

In our study, because isometric MVC torque was unchanged throughout the fatigue task for the old men the reduction in peak power seems to be related to impairments in the maximal voluntary shortening velocity component, whereas for the young the 21% impairment in isometric MVC torque may be the greater contributor to their, albeit lesser decline in peak power. Thus a decrease in peak power output may be related mainly to a reduction in torque production in some tasks, but a decrease in peak shortening velocity can be of greater importance in other tasks or models (2), such as older adults performing fast dynamic shortening contractions. During isometric fatiguing tasks, it seems that older adults rely more on oxidative phosphorylation than young adults, irrespective of blood flow (26). This lower glycolytic flux may lead to less ATP cost and more ATP generated through oxidative processes (25), thus leading to less acidosis and accumulation of H_2PO_4^- , and mitigating isometric MVC torque reduction (24). Dynamic shortening contractions on the other hand are more metabolically costly than isometric contractions (32), and cross-bridge function in aged adults may be impaired as demonstrated by slower contractile kinetics (13). Support for these ideas can be found in the present study in which throughout the fatigue task, there was a negative association ($R^2 = 0.29$) between HRT and shortening velocity in both groups combined. This relationship has been reported previously only for young adults (9), and although stronger ($r = -0.85$) and in a different muscle group (knee extensors), it indicated that shortening velocity performance could be influenced by similar fatigue processes as those which affect the isometric twitch HRT. The slower contractile properties following the fatigue task likely are affected by age-related impairments in Ca^{2+} handling, which may have led to a greater attenuation in cross-bridge cycling, more specifically, a greater slowing in actin-myosin interaction (41) and a slower rate of cross-bridge dissociation (10). Details of possible metabolic factors and their alterations during dynamic contractions between young and old adults are not known but would help to further this understanding.

In addition to intrinsic age-related contractile slowing of the muscle, a more compliant tendon (28) of the old men also may contribute to slower joint kinetics and greater power loss. Thus, although slower contractile function of the musculoskeletal system may lead to enhanced fatigue resistance in the old men during isometric tasks (24), as expressed by the age-related leftward shifts in the torque-velocity (37) and torque-frequency (3) relationships, these may impair velocity-dependent performance in the old men during fast dynamic contractions.

Finally, although age-related musculoskeletal property changes combined with the higher metabolic cost of fast dynamic contractions may account for the greater fatigue in aged subjects, differences in muscle membrane excitability cannot be overlooked. In this study, the smaller baseline M-wave amplitude for the old compared with the young declined following the fatigue task by 20% only in the old men, which resulted in a 26% smaller M-wave area in the old than the young. This finding is similar to another study that used dynamic fatiguing contractions, albeit during a slow isovelocity task of the dorsiflexors (6), to evaluate changes in the M-wave properties. For this study and ours we suggest that the loss of amplitude and

area indicate reduced sarcolemmal excitability in the old, whereas conduction velocity likely was not affected as M-wave durations for either age group were unaltered by fatigue. Thus, despite maintained voluntary activation, some of the greater loss of power in the old men than the young may be explained by reductions in sarcolemmal excitability during fatigue using this task.

Because our subjects were all recreationally active, these results cannot be generalized to sedentary populations, but despite the fact the older adults were recreationally active, they still exhibited greater fatigue than the young men throughout and following the experimental task. In summary, during repetitive unconstrained fast dynamic shortening contractions of the plantar flexors, reductions in shortening velocity and muscle membrane excitability may explain the greater loss of power experienced by the old men compared with the young, thus leading to an age-related increase in fatigue for this task.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

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