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The age-related slowing of voluntary shortening velocity exacerbates power loss during repeated fast knee extensions

Brian H. Dalton [a], Geoffrey A. Power [a], Anthony A. Vandervoort [a,b], Charles L. Rice [a,c,*]

[a] Canadian Centre for Activity and Aging, School of Kinesiology, The University of Western Ontario, London, Ontario, Canada
[b] School of Physical Therapy, Faculty of Health Sciences, The University of Western Ontario, Canada
[c] Department of Anatomy and Cell Biology, The University of Western Ontario, London, Ontario, Canada

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ABSTRACT

Older adults are less fatigable than young during isometric tasks, but this apparent ability to resist fatigue is often abolished when dynamic actions are performed. These findings could indicate that the velocity component of dynamic contractions or the task performed is an important factor in explaining fatigability of older adults. However, it has not been evaluated systematically. The purpose was to investigate the differences in age-related fatigue of the knee extensors in 8 older (73.6 ± 3.5 years) and 8 younger (25.1 ± 2.6 years) men. Neuromuscular measures were collected at baseline, during and immediately following task termination of three different maximal effort knee extension tasks. On three separate days, participants performed either 30 slow ($1.05\ \mathrm{rad\cdot s^{-1}}$, $60°\cdot\mathrm{s}^{-1}$) or 30 moderate ($3.14\ \mathrm{rad\cdot s^{-1}}$, $180°\cdot\mathrm{s}^{-1}$) isovelocity contractions, or 30 fast unconstrained velocity contractions with a fixed resistance (i.e., 20% maximal voluntary isometric contraction). At baseline, the older men were 25% and 35% less powerful than the younger men for the slow and moderate isovelocity tasks, respectively, but 42% less for the fast unconstrained velocity protocol. At task termination for the slow (old: 53%, young: 53%) and moderate (old: 45%, young: 38%) isovelocity fatigue tasks, power was reduced similarly in both age groups. However, for the fast unconstrained velocity task, power was reduced by a greater extent in older (35%) than the younger men (23%) at task termination. These results highlight that age-related impairments in voluntary shortening velocity exacerbate reductions in power production during repetitive dynamic tasks. Furthermore, the importance of this factor is masked when velocity is constrained (isovelocity) and fatigue is dependent primarily upon slow torque generation.

1. Introduction

Adult aging is accompanied by various alterations in the neuromuscular system that lead to reductions in strength and power, and ultimately muscle function (Aagaard et al., 2010). Age-related architectural (Narici and Maganaris, 2007) and functional (Hunter et al., 1999) changes contribute to a slowing in whole muscle contractile properties resulting in a leftward shift in the torque–frequency relationship (Roos et al., 1999). Slowed isometric contractile properties may allow for more economical muscle activation through reduced motor unit discharge rates (Dalton et al., 2010a) and therefore lower ATP turnover (Kent-Braun, 2009) in older adults. Thus, during relative isometric fatiguing tasks older adults are less fatigable than younger adults (Kent-Braun, 2009).

When contractile velocity is included with measures of strength (torque), power (i.e. torque × velocity) can be calculated to assess muscle capacity during a dynamic fatiguing task. For dynamic contractions, conflicting reports suggest that older adults are more fatigable (Dalton et al., 2010b; Petrella et al., 2005), less fatigable (Lanza et al., 2004; Rawson, 2010), or even similar (Callahan et al., 2009; Laforest et al., 1990) when compared with younger adults. Furthermore, the relatively few studies on fatigue and aging have focused more on the force or torque (i.e., isovelocity tasks) component of power, rather than velocity. During these tasks, velocity is constrained (i.e., pre-set) and changes in power are related directly to alterations in torque production, despite shortening velocity being a key component strongly related to the inherent design properties of skeletal muscle (Lieber and Ward, 2011).

For most all studies on age-related fatigue during dynamic tasks, the knee extensors have been utilized (Petrella et al., 2005; Rawson, 2010; Callahan et al., 2009; Laforest et al., 1990; Aniansson et al., 1978; Deschenes et al., 2008; Larsson and Karlsson, 1978; Lindstrom et al., 2006, 1997), but those studies were limited to slow and moderate knee extension tasks ($1.57–4\ \mathrm{rad\cdot s^{-1}}$). Indeed, during

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Abbreviations: ANOVA, Analysis of Variance; ATP, Adenosine triphosphate; EMG, Electromyography; ES, Effect size; HRT, Half relaxation time; M-wave, Compound muscle action potential; MVC, Maximal voluntary isometric contraction; ROM, Range of motion; TPT, Time to peak twitch torque.

[*] Corresponding author at: Canadian Centre for Activity and Aging, School of Kinesiology, Faculty of Health Sciences, Arthur and Sonia Labatt Health Sciences Building, The University of Western Ontario, London, Ontario, Canada, N6A 5B9. Tel.: +1 519 661 1628; fax: +1 519 661 2008.
E-mail address: crice@uwo.ca (C.L. Rice).

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natural gait, knee angular velocities can reach ≥6.7 rad·s^{-1} in older and younger adults (Jevsevar et al., 1993). However, these faster velocities have not been tested using the isovelocity paradigm. This is because older adults are not capable of producing a reliable torque output throughout a full range of motion (ROM) at knee extension velocities greater than 4.71 rad·s^{-1} (Lanza et al., 2003) during constrained isovelocity tasks.

It is clear from these studies that an important variable not properly or thoroughly explored is the effect of voluntarily controlled shortening velocity on age-related fatigability. Utilizing a fatigue task with a relative fixed resistance (i.e., % MVC) and subject-dependent unconstrained shortening velocity should provide a more meaningful and practical assessment of power loss during a dynamic fatigue task, especially when the task is performed at moderate to high joint angular velocities. One challenge in assessing power loss during fatigue is to understand the relative contribution from each factor (i.e., torque and velocity) without the confounding effects of ROM failure, which is an important variable to consider when assessing dynamic muscle performance (Cheng and Rice, 2010). Therefore, an alternate and complementary paradigm is required to overcome these limitations and to evaluate fully the influence and importance of velocity during dynamic tasks in older adults.

Furthermore, a major limitation of extracting meaningful results from previous studies investigating age-related fatigue during dynamic tasks include: differences in the ages of participants, muscle groups tested, and experimental protocols. Because of the task-dependent nature of fatigue (Hunter, 2009) and the inconsistencies among protocols it is difficult to draw conclusions based upon the equivocal results presented in the literature. Importantly, no study has compared in the same subjects different velocity paradigms to fully evaluate the importance of shortening velocity on age-related fatigue

To resolve some of the above discrepancies between testing modalities and to better understand the effect of voluntary shortening velocity on power loss during fatigue, we designed a study in which the same participants performed three different dynamic fatiguing protocols at different contractile velocities. To alter velocity using a constant resistance that could be moved through a complete ROM for several contractions we used a combination of isovelocity and unconstrained velocity paradigms (further explained in Materials and methods). Due to inherent age-related contractile slowing (Roos et al., 1999; Dalton et al., 2010b), this model is helpful to test the influence of velocity on power loss during dynamic fatiguing contractions in comparison with younger adults possessing faster contractile function. We expected that the older men would exhibit less fatigue (less power loss) than the younger men during a slow (1.05 rad·s^{-1}) isovelocity task because these dynamic contractions would be less affected by factors that impair velocity and thus similar to an isometric task (0 velocity). During a moderate isovelocity task (3.14 rad·s^{-1}) we hypothesized fatigue would be similar between age groups because velocity impairments would have an increased influence and thus compete with those factors that provided an advantage to older men when the task is isometric or slow. However, during the fast unconstrained velocity actions (>4 rad·s^{-1}) the older men would exhibit greater fatigue than their younger counterparts because impairments in muscle contractile speed and shortening velocity would be the main factors responsible for the loss of power.

2. Materials and methods

2.1. Participants

Eight older men (age: 73.6 ± 3.5 years, height: 175.8 ± 4.4 cm, body mass: 85.0 ± 9.6 kg) and eight younger men (age: 25.1 ± 2.6 years, height: 175.4 ± 8.2 cm, body mass: 77.8 ± 13.1 kg) volunteered for this study and completed all fatigue protocols. To eliminate sex-related differences as a covariate of the muscle fatigue response (Hunter, 2009) this study included only men. The older participants were recruited from a local activity group designed to maintain flexibility, muscle endurance and cardiovascular fitness through regularly scheduled exercise classes three times per week. The younger men, recruited from the university population, were not systematically trained and participated in moderate exercise approximately three times per week. All participants reported they were healthy and recreationally active with no evidence of neuromuscular disease. Oral and written informed consent was obtained from each participant prior to experimental testing. The local university's ethics review board for experimentation on humans approved the study and all procedures conformed to the Declaration of Helsinki.

2.2. Experimental arrangement

A Biodex System 3 multi-joint dynamometer (Biodex Medical Systems, Shirley, NY) was used to record knee extensor torque, knee position and velocity in the isometric, isokinetic and isotonic modes with all tests performed on the right (dominant) leg. Participants were seated comfortably in an upright position with the hip angle at ~100° (~1.74 rad). The knee angle was set at 90° (1.57 rad) for all isometric measures. Range of motion for all dynamic contractions was set at 90°. The initial position for all dynamic knee extensions was set at 90° from terminal knee extension. To minimize extraneous body movements, the participants were fastened securely to the chair with inelastic straps around the shoulders, hips and right thigh. The knee joint was aligned with the axis of rotation of the dynamometer and an inelastic strap, ~2 cm superior to the malleoli, secured the leg to the dynamometer knee attachment. All knee extensor 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).

To assess isometric contractile properties, voluntary activation and sarcolemma excitability, electrically evoked twitches and compound muscle action potentials (M-waves) were elicited from the knee extensors using two custom-made aluminum electrode pads at a knee angle of 90° (1.57 rad). These electrodes were wrapped in thin conductive gel-soaked paper towel and applied transversely to the thigh with cloth tape. One electrode was positioned ~7 cm distal to the greater trochanter of the femur and the other was positioned ~6 cm distal to the inferior edge of the proximal stimulating electrode. Depending on the size of the thigh and to ensure the greatest muscle mass activation of knee extensors without activation of antagonist muscles, the stimulating electrode pad sizes varied accordingly (8–11 × 16–20 cm). Visual inspection and palpation was used to ensure only the knee extensors were activated by the electrical stimulation. Single stimuli were generated via a 100-μs square wave pulse set at a maximal voltage of 400 V (Digitimer stimulator, model DS7AH; Digitimer Ltd., Welwyn Garden City, UK).

Surface electromyography (EMG) signals were recorded from the vastus medialis using self-adhering surface pediatric cloth electrodes (H59P Repositionable Monitoring Electrodes; Kendall, Mansfield, Massachusetts). To minimize a stimulation artifact in the M-wave response and to ensure proper stimulation pad placement, EMG signals were recorded only from the vastus medialis. Prior to electrode placement, the skin was cleaned with alcohol. Using a 3 cm inter-electrode distance, an electrode pair was positioned over the vastus medialis muscle belly in parallel with the muscle fibers and a ground electrode was positioned over the right patella. Surface EMG signals were preamplified (×100), amplified (×2), bandwidth filtered (10 Hz to 1 kHz), converted by a 12-bit analog-to-digital converter (Power 1401, Cambridge Electronic Design), and sampled on-line at 2000 Hz.

2.3. Experimental procedures

Data were collected over three visits to the neuromuscular laboratory, in which a randomly selected dynamic knee extension fatigue protocol was performed during each occasion. Apart from the fatigue protocol, testing procedures were identical for each visit. Test sessions were separated by at least three days to account for any residual fatigue, but no more than seven days.

After participant set-up, an M-wave from the vastus medialis and an associated knee extensor (whole quadriceps) twitch were elicited. The stimulus current was increased progressively until there was no further appreciable increase in amplitude of the M-wave or twitch. The current was then increased an additional 10% to ensure all motor axons were activated, but with no reduction in knee extensor twitch torque that might indicate activation of antagonist muscles. Next, the participants performed three ~5 s maximal isometric MVCs. An additional MVC was attempted if the first three varied in peak torque amplitude by more than 5%. All MVCs included a supramaximal twitch delivered ~1 s before (at rest), another during the peak plateau of MVC torque (T_s) and another ~1 s following (T_r) when the knee extensors were relaxed fully. Twitch amplitudes during and after each isometric MVC were used to assess voluntary activation of the knee extensors via the interpolated twitch technique {% activation $=[1-(T_s/T_r)]\times 100$}. All participants were exhorted during the maximal voluntary attempts and provided visual feedback of the torque tracing via computer monitor. All isometric MVCs were separated by at least 3 min of rest.

Three minutes following the isometric MVC attempts, the participants were familiarized to the maximal effort dynamic shortening contractions to be performed that day. Depending on the testing session, the shortening contractions involved either one of three maximal effort tasks. The isovelocity (isokinetic mode of the Biodex) tasks included slow (1.05 $\text{rad}\cdot\text{s}^{-1}$, 60°$\cdot\text{s}^{-1}$) or moderate (3.14 $\text{rad}\cdot\text{s}^{-1}$, 180°$\cdot\text{s}^{-1}$) speed contractions. Whereas the unconstrained velocity (isotonic mode of the Biodex) task was dependent upon how fast a participant could voluntarily move a fixed resistance of 20% MVC. During pilot testing, it was found that at 20% MVC all participants could maintain full ROM of the task, despite significant decreases in power production. At higher loads, we could not be certain that all older subjects would be able to complete the task. From pilot testing, loads at or beyond 40% of isometric MVC could not be successfully maintained for more than a few contractions without ROM failure in most subjects. Thus, for concentric dynamic contractions requiring maximal efforts, a load of 20% MVC represents a moderate resistance. Although contractions in the isotonic mode are not strictly by definition isotonic, this mode, through a mechanical braking system that is not influenced by gravity, allows the torque to be dependent on the velocity of the contraction which is controlled by the participant's capacity, and not by the dynamometer. All tasks were performed through a 1.57 rad (90°) ROM. During all dynamic efforts participants were instructed to move the dynamometer "as fast and as hard as possible". All participants were provided the same scripted verbal encouragement throughout the task. Visual feedback of the velocity and torque profiles was displayed on a computer monitor (Fig. 1). After completing a shortening contraction, the participant relaxed fully and the dynamometer passively returned the leg back to the original starting position at a speed of ~2.62 $\text{rad}\cdot\text{s}^{-1}$ (150°$\cdot\text{s}^{-1}$) for all dynamic contraction types. Familiarization involved ~5–10 dynamic contractions separated by short rest intervals of ~5–10 s. Once a consistent peak velocity or torque was achieved (no change during 5 consecutive attempts), the participants performed 5 consecutive shortening contractions at the pace involved in the fatigue protocol. The familiarization portion of the session was followed by 3 min of rest. Then, the participants performed the fatigue task.

For all testing paradigms, the fatigue task consisted of 30 maximal effort dynamic shortening contractions. Immediately following the 30th dynamic contraction, an isometric MVC and corresponding evoked measures (described above) were performed. Three fatigue paradigms were used to fully explore velocity and to allow comparisons with previous studies whose results indicate inconsistent findings on age-related fatigability during dynamic tasks. For slow (1.05 $\text{rad}\cdot\text{s}^{-1}$) and moderate (3.14 $\text{rad}\cdot\text{s}^{-1}$) velocities we used an isokinetic paradigm. For the fast velocities we used an unconstrained velocity task (isotonic mode) with a fixed load of 20% MVC. To achieve slow and moderate velocities using an unconstrained velocity would have required increasing the resistance to the point that the fatiguing task duration would have been decreased substantially and induced ROM failure, especially in the older men. Additionally, older participants are unable to generate reliable maximum torque through a full range of motion when the pre-determined velocity of knee extension is $\geq 4.71\ \text{rad}\cdot\text{s}^{-1}$ (Lanza et al., 2003). Thus, different contraction modes were utilized for the dynamic shortening fatigue paradigms. Finally, the baseline power values were similar between the moderate isovelocity and the unconstrained velocity tasks permitting a novel direct comparison of fatigue using these different tasks with equal power.

2.4. Data analysis and statistics

To provide an indication of sarcolemmal excitability and neuromuscular propagation, peak to peak amplitude, duration, and area (the area under the negative and positive peaks) of the vastus medialis M-wave were analyzed. Inherent changes in the isometric contractile function of the knee extensors was assessed by peak twitch torque (Nm), time to peak twitch torque (TPT; ms), and half relaxation time (HRT; ms) of the twitch.

The baseline isometric MVC peak torque and all corresponding electrically evoked contractile property values were taken from the MVC with the maximum torque of the pre-fatigue attempts. Baseline dynamic torque and power were taken from the maximum torque value for the isovelocity contractions. Baseline shortening velocity and peak power of the unconstrained velocity task were taken from the contraction with the maximum velocity. Peak dynamic values occurred within the first five contractions of the fatigue protocol. For the isovelocity tasks, power (W) was calculated as the product of the peak torque generated by the participant (Nm) and the pre-set velocity ($\text{rad}\cdot\text{s}^{-1}$) of the dynamometer. For the unconstrained velocity movements, power (W) was calculated as the product of maximal shortening velocity ($\text{rad}\cdot\text{s}^{-1}$) and the pre-set external load (Nm) of the dynamometer. To compare results among the fatigue tasks, voluntary torque or velocity, and power of each dynamic task, were normalized to the respective baseline value and then an average was calculated over every five contractions.

To analyze isometric EMG data of the vastus medialis, the root mean square (RMS) value was calculated over a 1-s interval about the peak torque for the MVC following task termination and normalized to the RMS of the baseline MVC. For EMG analysis during the dynamic tasks, the RMS value was calculated over the full ROM of each shortening contraction and averaged over every 5 contractions. This value was then normalized to the RMS EMG from the baseline value.

Data were analyzed using SPSS version 16 (SPSS, Chicago, IL). To ensure baseline values of the isometric measures were not different from day-to-day, a one-way analysis of variance (ANOVA) was applied. Because there were no day-to-day differences, baseline values were pooled to test for age-related (group) differences. An unpaired t-test was used to compare all baseline values between groups, and relative change of all mechanical isometric measures and isometric surface EMG values as a result of the fatigue protocols, except for voluntary activation for which a non-parametric Mann–Whitney U-test was used to analyze group differences. A two-way ANOVA (age × time) with repeated measures was used to analyze all normalized mechanical and electrophysiological data from the dynamic fatigue protocols. The level of significance for all tests was set at $P \leq 0.05$. Post hoc analysis using paired (i.e., main effect for time) and unpaired (i.e., main effect for age or interaction) T-tests were performed with a Bonferonni 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

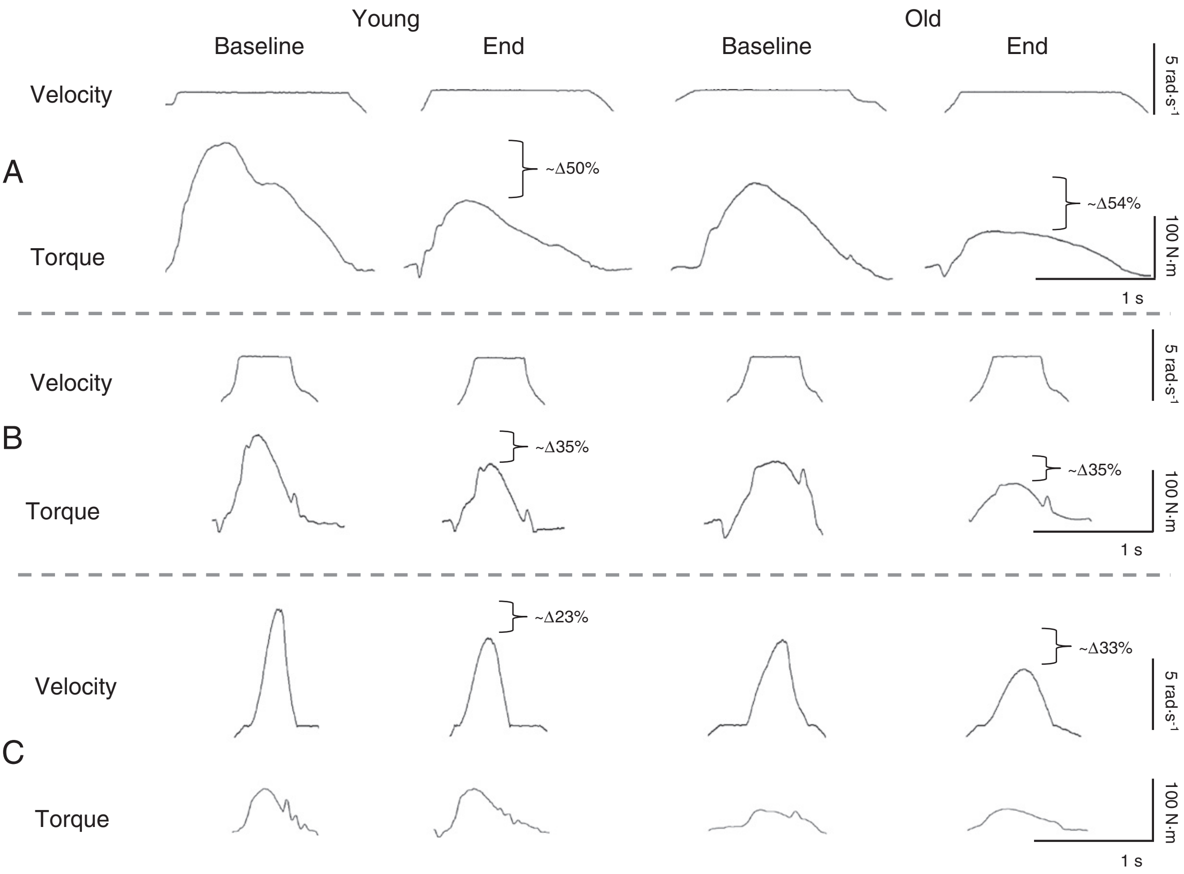

Fig. 1. Typical dynamic torque and velocity tracings at the beginning (contraction 2) and end (contractions 30) of the isovelocity task at 1.05 rad·s^{-1} (A), the isovelocity task at 3.14 rad·s^{-1} (B) and the unconstrained velocity task at a load of 20% isometric MVC torque (C) for one older and younger man.

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 the change in HRT and peak power during each fatigue task. Descriptive statistics are reported as means ± standard deviations (SDs).

3. Results

3.1. Voluntary baseline measures

All baseline isometric values were not different from day-to-day ($P>0.11$). Thus, these values were averaged over the three testing days for comparison between age groups. Despite equivalent voluntary activation (~96%) during the isometric MVC attempts, the older men were 27% weaker ($P<0.01$, ES = 0.40) than the younger men. The older men were also 25% and 35% weaker for dynamic strength during the slow (1.05 rad·s^{-1}; $P<0.01$, ES = 0.51) and moderate (3.14 rad·s^{-1}; $P<0.01$, ES = 0.99) speed isovelocity tasks, respectively. For the unconstrained velocity task, the older men were 20% slower ($P<0.01$, ES = 0.76) than the younger men (Table 1). Hence, peak power for the older men was 25%, 35%, and 42% less during the slow ($P<0.01$, ES = 0.52) and moderate ($P<0.01$, ES = 0.78) isovelocity tasks, and the unconstrained velocity task ($P<0.01$, ES = 0.96) compared with the younger men, respectively (Fig. 2). Baseline ROM for each task was similar between age groups ($P>0.18$).

3.2. Evoked neuromuscular baseline measures

The older men had a 43% lower peak twitch torque ($P<0.01$, ES = 0.73) with 7% slower TPT ($P<0.05$, ES = 0.38) than the younger men, but with no differences in HRT ($P=0.85$; Table 1). When normalized for the large differences in peak twitch torque, TPT and HRT were 88% ($P\leq0.01$, ES = 0.67) and 72% ($P\leq0.01$, ES = 0.57) slower for the older than younger men, respectively (Table 1). For the M-wave of the vastus medialis, peak to peak amplitude was 25% smaller ($P<0.05$, ES = 0.33) and duration was 113% longer ($P<0.01$, ES = 0.56) in the older men compared with the younger men, respectively. This resulted in no differences in M-wave area for both age groups ($P=0.30$).

Table 1
Baseline neuromuscular characteristics of the knee extensors. The older men were weaker and slower than the younger men (*$P<0.05$). Values are shown for maximal voluntary isometric contraction (MVC), voluntary activation (VA), peak twitch torque (Pt), time to peak twitch torque (TPT), half relaxation time of the twitch torque (HRT), TPT normalized to Pt, HRT normalized to Pt, maximal voluntary dynamic contraction torque at 1.05 rad·s^{-1} (MVDC$_{1.05}$), maximal voluntary dynamic contraction torque at 3.14 rad·s^{-1} (MVDC$_{3.14}$), and maximal voluntary velocity at a fixed load of 20% isometric MVC (Velocity). Values are means ± SD with 95% confidence intervals (CIs) for the difference in means.

Group (n = 8)	Young	Old	95% CI
MVC (Nm)	286.6 ± 59.8	210.5 ± 36.1*	−129.1, −23.1
VA (%)	95.3 ± 3.3	97.8 ± 1.2	−0.2, 5.1
Pt (Nm)	49.0 ± 8.1	28.0 ± 5.5*	−28.4, −13.6
TPT (ms)	107.6 ± 5.3	115.2 ± 5.0*	2.0, 13.1
HRT (ms)	91.0 ± 20.0	91.6 ± 29.6	−26.5, 27.7
Normalized TPT (ms·Nm^{-1})	2.3 ± 0.5	4.2 ± 0.9*	1.2, 2.8
Normalized HRT (ms·Nm^{-1})	1.9 ± 0.6	3.3 ± 0.7*	0.7, 2.1
MVDC$_{1.05}$ (Nm)	218.7 ± 29.5	163.2 ± 28.1*	−86.4, −24.6
MVDC$_{3.14}$ (Nm)	162.0 ± 20.1	105.0 ± 11.3*	−74.5, −39.6
Velocity (rad·s^{-1})	8.4 ± 0.5	6.7 ± 0.5*	−2.2, −1.1

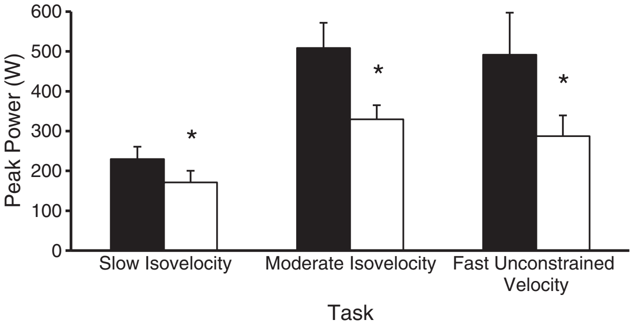

Fig. 2. Baseline peak power for three dynamic knee extensor tasks. The older (open) men were less powerful than the younger men (filled) for the isovelocity task at 1.05 rad·s^{-1} (slow isovelocity), the isovelocity task at 3.14 rad·s^{-1} (moderate isovelocity) and the fast unconstrained velocity task at a fixed load of 20% isometric MVC torque ($P<0.01$). Values are means ± SD.

3.3. Isovelocity fatigue tasks

For peak power during the 1.05 rad·s^{-1} task, there was a time effect ($P<0.01$, ES = 0.95) and an interaction ($P<0.05$, ES = 0.23) with no main effect for age ($P=0.17$). Thus, the older men had a progressive reduction in peak power from and including contractions 6 to 30 compared with baseline. However, the younger men had a progressive decrease in peak power for contractions 11 to 30 from baseline (Fig. 3A). For the 3.14 rad·s^{-1} isovelocity task, both the older and younger men had a progressive reduction in peak power from baseline for all contractions above and including contractions 11 to 15 (time effect: $P<0.01$, ES = 0.93); whereas the older men had lower peak power values than the younger for contractions 11 to 25 (age effect: $P<0.01$, ES = 0.53; interaction: $P<0.05$, ES = 0.23; Fig. 3B).

3.4. Unconstrained velocity fatigue task

For the fast unconstrained velocity task there were main effects for time ($P<0.01$, ES = 0.89) and age ($P<0.01$, ES = 0.57) with an interaction ($P<0.01$, ES = 0.28). This resulted in a 35% reduction in peak power by task termination for the older men and only 23% for the younger men, but with the older men exhibiting lower peak power than the younger men for contractions 6 to 30 (Fig. 3C). Overall, peak velocity declined from 6.7 ± 0.5 rad·s^{-1} to 4.4 ± 0.6 rad·s^{-1} and 8.4 ± 0.5 rad·s^{-1} to 6.5 ± 0.7 rad·s^{-1} in the older and younger men, respectively. The age-related differences in power were not confounded by any differences in ROM between groups throughout any fatiguing tasks ($P=0.33$–0.45).

3.5. Voluntary isometric fatigue measures

For both age groups, isometric MVC torque was reduced from baseline to 59.9 ± 9.1% following the slow isovelocity ($P<0.01$, ES = 0.96), 69.1 ± 6.7% following the moderate isovelocity ($P<0.01$, ES = 0.96), and 72.4 ± 7.7% following the unconstrained velocity ($P<0.01$, ES = 0.94) tasks. Isometric voluntary activation did not differ between age groups for any protocol ($P>0.11$), but was only reduced in both age groups by 5% and 4% following the slow ($P<0.01$, ES = 0.48) and moderate ($P<0.01$, ES = 0.46) speed isovelocity tasks, respectively.

3.6. Evoked isometric fatigue measures

For peak twitch torque, there were similar reductions for both age groups of 38%, 17%, and 14% for the slow and moderate isovelocity tasks, and the fast unconstrained velocity task, respectively ($P<0.05$, ES ≥ 0.34; Fig. 4). TPT did not differ from baseline or between age groups for the isovelocity tasks ($P \geq 0.07$), but TPT was lengthened by 8% following the unconstrained velocity fatigue task compared with baseline in the older men ($P<0.05$, ES = 0.47). There were no changes in TPT for the younger men ($P=0.11$; Fig. 4). Both age groups had a similar 28% lengthening of HRT following the slow ($P<0.05$, ES = 0.30) isovelocity task, but for the moderate speed isovelocity ($P<0.05$, ES = 0.31) and unconstrained velocity ($P<0.01$, ES = 0.46) tasks, only the older men had a 47% and 29% lengthening of HRT (Fig. 4).

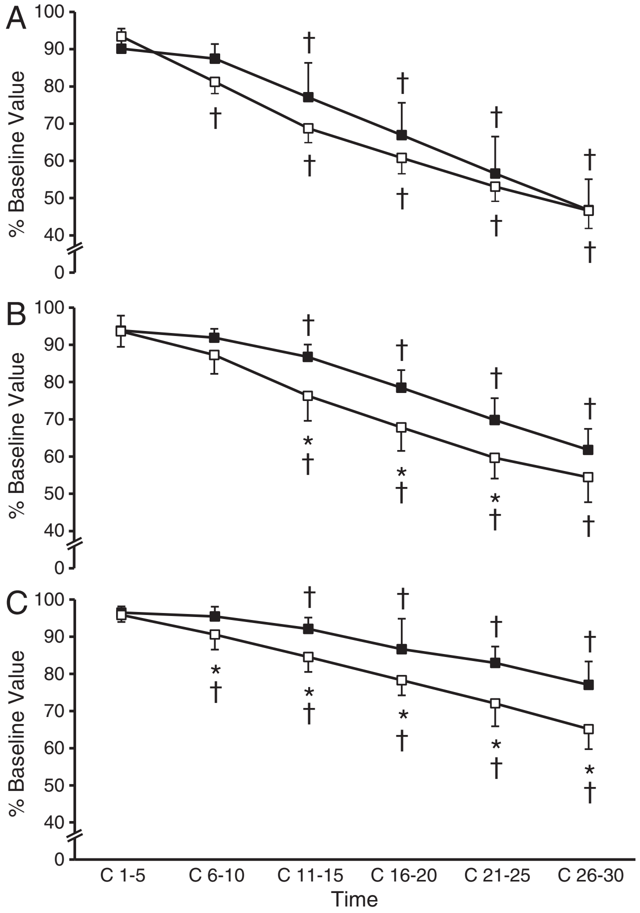

Fig. 3. Fatigue response of peak power during the isovelocity task at 1.05 rad·s^{-1} (A), the isovelocity task at 3.14 rad·s^{-1} (B) and the unconstrained velocity task at a load of 20% isometric MVC torque (C) for the older (open) and younger (filled) men. * denotes an age-related difference between the older and younger men ($P<0.05$). † denotes a difference from C 1–5 ($P<0.01$). C represents contractions. Values are means ± SD.

There was a moderate correlation ($r=0.50$, $P<0.05$) between the change in HRT and change in peak power following the unconstrained velocity fatigue task with a significant linear regression ($\text{power}_{(\%\ \text{change})} = -0.16 \cdot \text{half relaxation time}_{(\%\ \text{change})} + 25.75$, $R^2=0.25$, $P<0.05$). However, there were no significant correlations or regressions for change in HRT and change in power following the slow ($r=0.33$, $P=0.22$) and moderate ($r=0.02$, $P=0.94$) isovelocity fatigue tasks (Fig. 5).

3.7. Electromyographic fatigue measures

Peak to peak amplitude of the vastus medialis M-wave for both age groups was increased similarly in all three fatigue protocols ranging from ~107% in the slow isovelocity task to ~113% for the fast unconstrained velocity ($P \leq 0.05$, ES = 0.24–0.34) task. For both age groups, M-wave area increased to ~121% and ~110% following the moderate isovelocity ($P<0.01$, ES = 0.46) and fast unconstrained velocity ($P<0.05$, ES = 0.28) fatigue tasks, respectively, but was unchanged following the slow isovelocity task ($P=0.10$).

For both age groups, RMS amplitude of the vastus medialis surface EMG was unchanged throughout the slow (range: 91.3 ± 10.8% to 111.3 ± 40.3%) and moderate (92.1 ± 14.5% to 103.7 ± 27.6%) speed

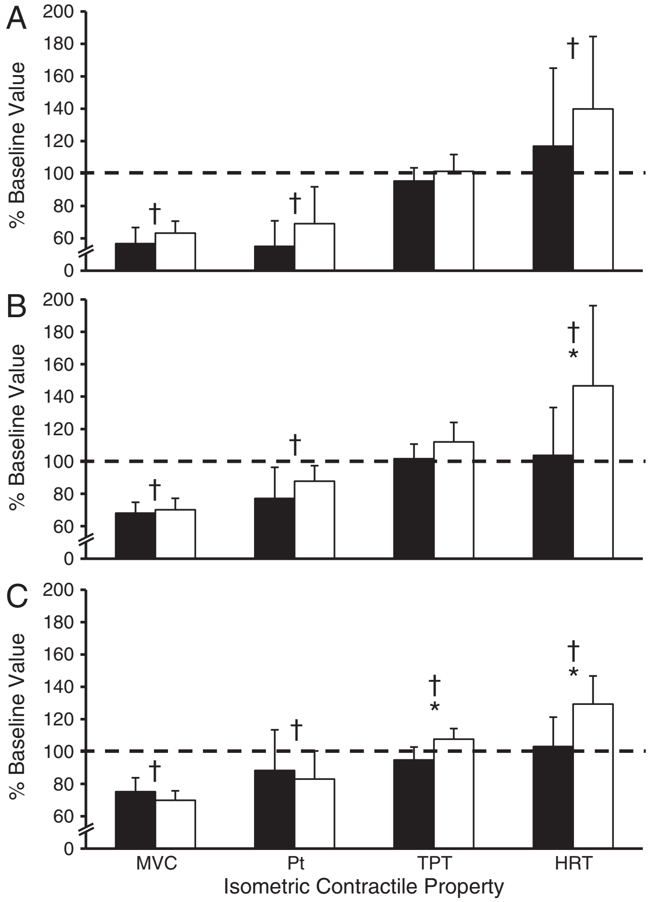

Fig. 4. Fatigue response of maximal voluntary isometric contraction torque (MVC), peak twitch torque (P_t), time to peak twitch torque (TPT), and half relaxation time (HRT) following the isovelocity task at 1.05 rad·s^{-1} (A), the isovelocity task at 3.14 rad·s^{-1} (B) and the unconstrained velocity task at a load of 20% isometric MVC torque (C) for the older (open) and younger (filled) men. * denotes an age-related difference between the older and younger men ($P<0.05$). † denotes a difference from baseline ($P<0.05$). The dashed line represents baseline values.

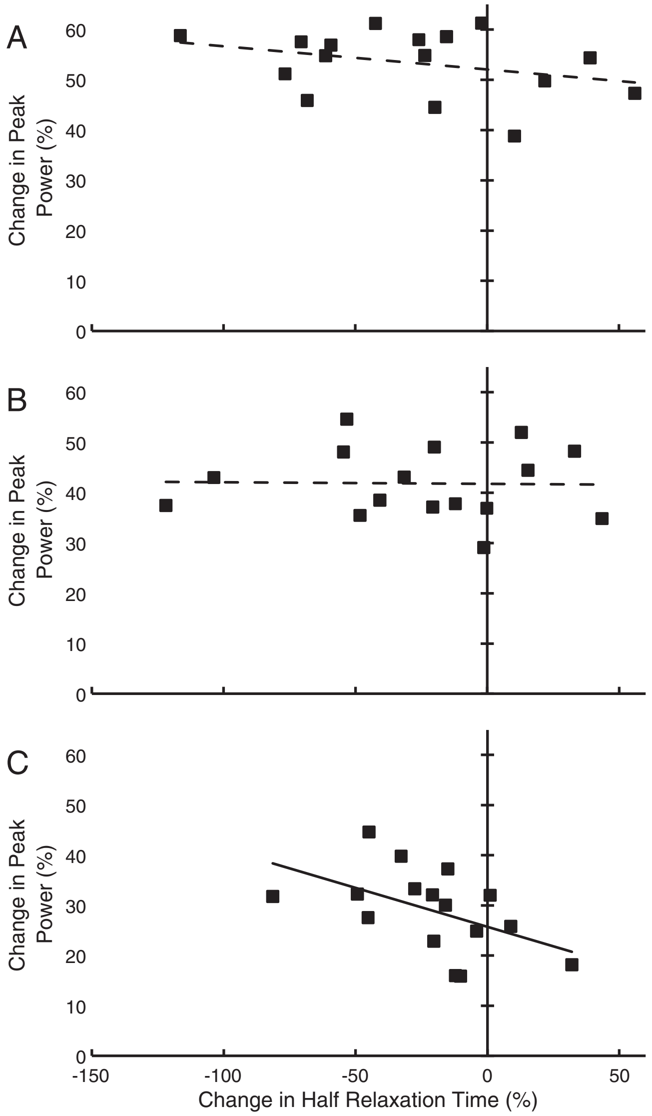

Fig. 5. Relationship between the change in half relaxation time of the evoked twitch and change in peak power following the 1.05 rad·s^{-1} (A) and 3.14 rad·s^{-1} (B) isovelocity tasks and the unconstrained velocity task at a load of 20% isometric MVC torque (C). There was only a significant association for the fast unconstrained velocity task ($r=0.50$, $R^2=0.25$, $P<0.05$).

isovelocity tasks, nor for the fast unconstrained velocity task (range: 95.8 ± 20.4 to 109.3 ± 39.9%). Vastus medialis RMS amplitude of the isometric MVC did not decline significantly from baseline following the moderate isovelocity (87.8 ± 38.7%) and fast unconstrained velocity tasks (89.5 ± 28.0%), but decreased similarly in both groups to 74.3 ± 28% following the slow speed isovelocity task.

4. Discussion

These experiments investigated the effect of varying dynamic contractile shortening velocity on fatigability in older and younger men. In agreement with our hypotheses, the weaker, slower, and hence, less powerful older men were more fatigable compared with the younger men during the fast (~6–9 rad·s^{-1}) unconstrained velocity knee extensor task. However, fatigue was similar between age groups for the slower isovelocity tasks (slow: 1.05 rad·s^{-1} and moderate: 3.14 rad·s^{-1}). The present study indicates that, in the same participants, as the shortening velocity of a task increased, the age-related advantage exhibited during isometric contractions (Kent-Braun, 2009) was reversed and fatigue was exacerbated in the inherently slower contracting muscles of the older men compared with young. Our experimental design recognized the importance of ROM and the limitations in testing the speed of contraction of older subjects during an isovelocity paradigm. Therefore, we were able to determine that the age-related impairments in shortening velocity are masked when the speed of contraction is constrained and older men are indeed more fatigable at faster velocities, even when baseline power is equated. The velocity component of muscle function represents a key design element during dynamic tasks (Lieber and Ward, 2011) and its attenuation through adult aging leads to critical impairments in muscle endurance during repetitive actions.

4.1. Baseline

Despite no differences in voluntary activation, the older men were 27%, 25% and 35% weaker than younger men for the isometric, and slow and moderate isovelocity maximal torque production efforts, respectively (Table 1). These age-related reductions in isometric and dynamic knee extensor torques are similar to previous reports (Roos et al., 1999; Petrella et al., 2005; Callahan et al., 2009; Lanza et al., 2003). The substantial slowing found for the electrically evoked contractile properties is supported by a ~20% slower velocity of shortening during the unconstrained velocity task in the older men compared with the young. This slowing of contractile function is in agreement with other reports in this muscle group (Roos et al., 1999; Petrella et al., 2005), and other limb muscles (Dalton et al., 2010b; McNeil and Rice, 2007;

Valour et al., 2003). As a result of slower and weaker voluntary and evoked contractions, the older men were 26–42% less powerful than the younger men during the different dynamic tasks (Fig. 2).

4.2. Fatigue

Power production is dependent upon the ability of the muscle to generate torque and shortening velocity. Additionally, repetitive dynamic performance is also dependent upon a muscle group to generate power throughout a ROM for successful completion of the task (Cheng and Rice, 2010). To properly compare the fatigue response between older (i.e., weaker) and younger participants among the three protocols it was important especially for the unconstrained fast velocity task to maintain equal and full ROM in both age groups. Thus, we used a moderate resistance of 20% MVC and indeed all subjects were capable of completing the tasks without ROM failure. A few studies (Dalton et al., 2010b; Petrella et al., 2005; McNeil and Rice, 2007; Power et al., 2011) have used unconstrained velocity tasks and reported greater power loss during fatigue in the older compared with younger adults, but they were limited by rather slow contractile shortening compared with the capacity of the knee extensors. Furthermore, no other studies have compared in the same subjects slow, moderate and fast velocities of shortening to address these questions systematically. Importantly, all tasks required maximal effort contractions and with this design we were also able to compare age-related fatigue at equal baseline powers between the moderate isovelocity and fast unconstrained velocity tasks.

At task termination of the slow and moderate isovelocity tasks, the older and younger men exhibited equal reductions in power (Fig. 3). These findings are similar to other studies, but not all (Rawson, 2010), in the knee extensors using various isovelocities in the slower domain of this muscle group, e.g. from 1.57 $\mathrm{rad \cdot s^{-1}}$ to 3.14 $\mathrm{rad \cdot s^{-1}}$ (Callahan et al., 2009; Laforest et al., 1990; Deschenes et al., 2008; Lindstrom et al., 1997). However, despite equal baseline peak power for the moderate isovelocity and unconstrained velocity tasks (Fig. 2), power was only reduced to a greater extent in the older men than the younger men when the speed of the shortening contractions was maximal (i.e., the unconstrained velocity task). Although the fastest velocity elicited greater fatigue in the older than the younger men, the comparison between the moderate isovelocity task and the fast unconstrained velocity task when baseline power was equated is important and indicates a limitation of the isovelocity testing paradigm. Therefore, our results demonstrate directly that shortening velocity is a critical component during dynamic fatigue of power and the age-related disadvantage is masked during tasks dependent upon torque generation at slow to moderate constrained velocities.

Because EMG RMS amplitudes of the vastus medialis during all the dynamic fatigue tasks in the current study were unaltered for both age groups, it seems that failure of neuromuscular activation was not an important factor in the reduction of power. This was corroborated by high isometric voluntary activation when tested immediately following all fatigue tasks for both age groups (>90%). Furthermore, a slight potentiation of the M-wave response following the fatigue protocols, irrespective of task, suggests the reduction in power production was not exacerbated by possible failure in sarcolemmal excitability or neuromuscular propagation. This is a similar finding to a previous report on M-wave responses following isovelocity (1.57 $\mathrm{rad \cdot s^{-1}}$) shortening contractions of the dorsiflexors (Lanza et al., 2004). However, following slow (0.87 $\mathrm{rad \cdot s^{-1}}$) isovelocity dorsiflexion (Baudry et al., 2007) and fast (~4–5 $\mathrm{rad \cdot s^{-1}}$) unconstrained velocity plantar flexion (Dalton et al., 2010b) tasks, sarcolemmal excitability was a small factor in explaining some of the greater age-related impairment of dynamic muscle performance. These discrepancies are likely related to the stress placed on the system or the muscle group tested. For example, our fatigue tasks consisted of 30 contractions, whereas the dorsiflexion task (Baudry et al., 2007) contained 150 contractions with a preloaded MVC, and the plantar flexion task (Dalton et al., 2010b) used 50 contractions. Regardless, the lack of age-related differences in EMG amplitude and M-wave results in the present study indicate that properties within the muscle are key factors in explaining the greater fatigue-induced power loss in the older than younger men during the fast shortening actions.

The above conclusions are supported by the findings that the older men had a greater slowing in both twitch TPT and HRT than the young following task termination for the fast unconstrained velocity task. For the moderate isovelocity task there was only a slowing in HRT in the older men and neither of these properties was affected differently between age groups following the slow isovelocity protocol (Fig. 4). Furthermore, we found a significant negative relationship between slowing of HRT and power for the fast unconstrained velocity task, but not for the slow or moderate isovelocity contractions (Fig. 5). A study by Cheng et al. (Cheng and Rice, 2005) reported a strong negative relationship between changes in HRT and voluntary loaded shortening velocity in the knee extensors of young men after fatigue, and we reported a comparable relationship for plantar flexion in both older and younger participants (Dalton et al., 2010b). These relationships indicate that loaded shortening velocity, and therefore power, could be influenced by similar fatigue processes as those affecting HRT, but are undetected during isometric and slower isovelocity actions. Prolongation of muscle relaxation time for an isometric contraction following a high-intensity fatigue task is indicative of a slowing in calcium uptake or alteration in cross bridge kinetics (Jones, 2010). However, the mechanisms that affect isometric torque generation capacity and shortening velocity are different (Allen et al., 2008). That is, the reductions in isometric torque result from impairments in sarcoplasmic reticulum calcium handling (Cairns and Lindinger, 2008; Debold et al., 2006; Powers and Jackson, 2008); whereas velocity is impaired directly by sarcomere function due to combined factors of an increase in $[\mathrm{ADP}]_\mathrm{i}$ (Westerblad et al., 1998) and $[\mathrm{H}+]_\mathrm{i}$ (Debold et al., 2008), thus progressively increasing myosin phosphorylation, which can slow cross bridge cycling rates (Stewart et al., 2009). Thus, it appears that depending on the task performed, the contributing factors involved in power production may be dominated by a reduction in torque (i.e., slow isovelocity task); whereas for other tasks the key factors may relate to the reduction in shortening velocity (Allen et al., 2008). Therefore, in older adults factors relating to shortening velocity may be of greater importance than torque per se.

Following all three dynamic fatigue tasks in the current study, voluntary and electrically evoked isometric torques were reduced similarly for the older and younger men. This finding corroborates the results from the few other isovelocity studies (Callahan et al., 2009; Baudry et al., 2007), and extends these observations to now include a fast velocity task in the knee extensors. Because the older men had a greater disadvantage during the repeated fast actions than their younger counterparts (i.e. greater power loss) but a similar reduction in isometric torque following task termination, specific processes involved in cross bridge cycling may be the key limiting factor in the age-related maintenance of power production, especially at faster velocities. In addition to intrinsic impairments in contractile function, shortening velocity may be reduced by increased musculotendinous compliance with adult aging (Narici and Maganaris, 2007), which may dampen the transmission of muscular force from the muscle to tendon. Indeed, the overall result is expressed by the age-related slowing in electrically evoked and voluntary contractile properties (Table 1) causing a leftward shift in the torque–velocity relationship (Raj et al., 2010). This relationship, compromised by aging, indicates that the older men are more susceptible to fast velocity tasks than the younger men. Thus, the added stress of fatigue on the aged system would further alter the torque–velocity relationship; whereby optimal velocity at moderate loads (i.e., 20% MVC) would decrease to a greater extent in the older than younger men in order to produce maximal power.

During isometric tasks, in which older adults are less fatigable than younger adults (Kent-Braun, 2009), it seems that older individuals rely more on oxidative phosphorylation and less on glycolysis compared with their younger counterparts (Lanza et al., 2007). This greater fatigue resistance may be due to an age-related increase in a greater proportion of type I muscle fiber area compared with type II fiber area (Lexell et al., 1988). Therefore, lower glycolytic flux may lead to less ATP cost and more ATP generated through oxidative processes, leading to less acidosis and accumulation of $H_2PO_4^-$ (Kent-Braun, 2009). An age-related 'matching' of a reduction in motor unit discharge rates and slowed whole muscle contractile speed has been suggested (Kent-Braun, 2009) as one explanation for the lower ATP cost, although all muscles do not follow this paradigm (Dalton et al., 2010a, 2009). However, dynamic shortening contractions are known to be more metabolically costly than isometric contractions (Newham et al., 1995), and this increased energetic cost may alter the age-related metabolic advantage available during isometric tasks. This advantage may be mitigated during slow and moderate isovelocity tasks, and as shown here even reversed during faster shortening actions because a slower contracting muscle impedes performance that is dependent upon relatively rapid shortening velocities. It seems therefore that, impairments in repetitive dynamic shortening actions are exacerbated in older men as the speed of the task increases.

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