Effects of age and muscle action type on acute strength and power recovery following fatigue of the leg flexors

Brennan J. Thompson · Eric C. Conchola ·
Matt S. Stock

Received: 25 May 2015 / Accepted: 14 October 2015 / Published online: 3 November 2015
© American Aging Association 2015

Abstract Short-term strength and power recovery patterns following fatigue have received little research attention, particularly as they pertain to age-specific responses, and the leg flexors (i.e., hamstrings) muscle group. Thus, research is warranted addressing these issues because both age-related alterations in the neuromuscular system and mode of muscle action (e.g., eccentric, concentric, isometric) may differentially influence recovery responses from fatigue. The aim of this study was to investigate the strength and power recovery responses for eccentric, concentric, and isometric muscle actions of the leg flexors in young and older men following an isometric, intermittent fatigue-inducing protocol. Nineteen young (age=25±3 years) and nineteen older (71±4) men performed maximal voluntary contractions (MVCs) for eccentric, concentric, and isometric muscle actions followed by a fatigue protocol of intermittent (0.6 duty cycle) isometric contractions of

the leg flexors at 60 % of isometric MVC. MVCs of each muscle action were performed at 0, 7, 15, and 30 min following fatigue. Peak torque (PT) and mean power values were calculated from the MVCs and the eccentric/concentric ratio (ECR) was derived. For PT and mean power, young men showed incomplete recovery at all time phases, whereas the older men had recovered by 7 min. Eccentric and isometric muscle actions showed incomplete recovery at all time phases, but concentric recovered by 7 min, independent of age. The ECR was depressed for up to 30 min following fatigue. More rapid and pronounced recovery in older men and concentric contractions may be related to physiological differences specific to aging and muscle action motor unit patterns. Individuals and clinicians may use these time course responses as a guide for recovery following activity-induced fatigue.

Keywords Elderly · Hamstrings · Low frequency fatigue · Isometric · Eccentric · Concentric

B. J. Thompson (✉)
Neuromuscular Research Laboratory, Department of Kinesiology
and Health Sciences, Utah State University, Logan, UT, USA
e-mail: brennan.thompson@usu.edu

E. C. Conchola
Applied Musculoskeletal and Human Physiology Research
Laboratory, Oklahoma State University, Stillwater, OK, USA

M. S. Stock
Human Performance Laboratory, Texas Tech University, Lubbock,
TX, USA

Introduction

During the process of normal aging, the neuromuscular system undergoes a number of changes. These changes include the loss of muscle mass and Type II muscle fibers, muscle metabolism alterations and slowing of contractile properties, motor unit and neuromuscular junction remodeling, and motor unit activation impairments (Kamen et al. 1995; Lanza et al. 2007; Deschenes

2011), which may impact a variety of functional outcomes in human movement.

One particular area that has garnered attention in recent years is the effects of aging on the nature of muscle fatigue. Age-related changes in the neuromuscular system may influence the attributes of fatigue, which interestingly, may yield a favorable advantage in older adults (Kent-Braun 2009; Christie et al. 2011). Although a number of investigations have examined the influence of age on fatigue resistance capacities, as well as the associated mechanisms of distinct responses (Kent-Braun 2009; Christie et al. 2011), far fewer studies have investigated the age-related differences in recovery responses from voluntary contraction-induced fatigue. Bilodeau et al. (2001) fatigued the forearm flexors in young and older adults using a maximal voluntary contraction (MVC) until the torque dropped below 50 % of the MVC and assessed strength recovery at six recovery time periods for up to 20 min following the fatigue protocol. The authors reported incomplete recovery of strength at 20 min post exercise, with no differences between age groups; however, they acknowledged the findings may be influenced by a low number of subjects. Allman and Rice (2001) also examined age-related effects of voluntary isometric force during a recovery period following fatigue of the forearm flexors; however, they induced fatigue with an intermittent submaximal fatigue protocol. Similarly, they showed no differences between young and older men in force recovery responses during 60 min of recovery, with an incomplete recovery of force at 60 min in both groups. Likewise, their study sample size was small, with only seven subjects per group. Because both of these studies were performed on the elbow flexors, our understanding on other muscle groups is limited, such as whether these effects are also observed on the functionally important locomotor muscles of the lower body. Specific characteristics of the time-course responses during the short-term recovery period following neuromuscular fatigue are imperative to help provide clinicians with information on the likelihood of performance deficits at specified time periods.

Human movement activities, particularly those involving locomotion, involve the performance of concentric, eccentric, and isometric muscle actions (Gray and Chandler 1989; Hortobagyi et al. 1995), which may function synergistically (co-contraction of opposing muscle groups during dynamic contractions) or cyclically (muscle switching roles from concentric,

isometric, and eccentric actions during a movement cycle, for example, during gait). It has been suggested that differences in neural activation strategies exist between muscle actions, with eccentric actions exhibiting reduced activation and discharge rates, and selective activation of high threshold motor units (Enoka 1996). A common approach used by previous studies (Smith and Newham 2007; Iguchi and Shields 2010) has compared differences in fatigue responses when performing fatigue protocols using characteristically different eccentric vs. concentric muscle actions to elucidate mechanistic fatigue features unique to each type of muscle action; however, little if any attention has been given to the inverse approach in which fatigue is induced from a singular muscle action fatigue protocol (e.g., isometric muscle actions) and subsequently assessed for the effects on force characteristics specific to each of the three different muscle actions. It remains to be determined how neuromuscular fatigue induced from a controlled isometric muscle action protocol may uniquely impact each of the three muscle action types during an acute recovery period. This would shed light on the specific outcomes of fatigue recovery pertaining to each of the types of muscle actions that are all, at least to some extent, used for many common human movement tasks.

A particularly useful variable to assess these responses may be the eccentric/concentric ratio (ECR), which has been shown to be a sensitive measure in discriminating clinical conditions (Bennett and Stauber 1986; Marshall et al. 2010). The utility of this variable was recently demonstrated by Marshall et al. (2010) who found that neither concentric nor eccentric hamstrings strength was different between healthy controls and low back pain patients, whereas the ECR successfully identified the low back pain group from the control group. Although its use may be relatively validated in clinical populations, it has not been investigated in regard to the effects that fatigue may have on this variable, especially considering it is largely unknown how eccentric muscle performance during recovery periods may be impacted by fatiguing activities. Although some evidence suggests that eccentric strength is relatively well maintained during the actual performance of repetitive eccentric high force voluntary contractions (Tesch et al. 1990; Westblad et al. 1995), other data involving more sport-specific fatigue protocols shows higher post exercise strength deficits in eccentric vs. concentric strength as well as decreased functional (i.e., eccentric/concentric) hamstrings to quadriceps

strength ratios (Greig 2008; Small et al. 2010). We know of no studies examining responses of these specific parameters during short-term recovery periods. Finally, given that older adults have a relative preservation of eccentric strength in comparison to losses of concentric strength (Hortobagyi et al. 1995), the influence of fatigue and age on the eccentric and concentric performances may provide interesting insight into the complexity of these interactions with implications for performance deficit risks during acute recovery periods.

Clinically relevant implications of muscle fatigue may be prevalent in both young and older populations as a result of performing activities of daily living, exercise, and/or rehabilitation tasks (Conchola et al. 2013). Importantly, declines of neuromuscular function, which may occur following fatigue of the lower limbs, have been suggested to be a major risk factor for falls among the elderly (Bento et al. 2010). Also, these risks may be connected to the eccentric phase of muscle activities (Hortobagyi et al. 1995). Much of the efforts in understanding age-related fatigue resistance have been conducted during and/or immediately following occurrences of fatigue; however, few studies have examined the age-related effects—and associated mechanisms—of acute recovery patterns following fatigue in isometric vs. dynamic actions. Furthermore, no previous investigations have examined this topic in the mobility relevant leg flexor muscle group. Therefore, the purpose of this study was to investigate the strength and power recovery responses for eccentric, concentric, and isometric muscle actions of the leg flexors in young and older men following a fatigue-inducing bout of isometric, intermittent submaximal contractions. We hypothesized that no age-related differences would be observed in recovery responses following fatigue but that eccentric muscle actions would exhibit less recovery compared to concentric.

Methods

Subjects

Nineteen young (mean±SD: age=25±3 years; stature=179.1±8.1 cm; mass=89.0±22.0 kg) and nineteen older (age=71±4 years; stature=178.5±5.1 cm; mass=90.2±11.6 kg) healthy, recreationally active men volunteered to participate in the study. This study was approved by the University Institutional Review Board, and all

participants completed and signed an informed consent document and health history questionnaire prior to any testing. None of the subjects reported any current/ongoing neuromuscular diseases or musculoskeletal injuries of the knee or hip of their right leg within 1 year prior to testing.

Procedures

Subjects visited the laboratory on two occasions with the first session being a familiarization trial where all subjects were instructed on the procedures of the study and practiced the MVCs and the fatigue protocol (the familiarization fatigue protocol was performed for 90 s, which reached a challenging but not failure threshold for a majority of the subjects). Within 2–4 days following the familiarization trial, subjects reported back to the laboratory for the experimental testing trial. All subjects were instructed to refrain from any vigorous physical activity within 24 h and caffeine consumption within 12 h of experimental testing.

Maximal voluntary contractions

All MVCs were performed with the right leg using a calibrated Biodex System 4 isokinetic dynamometer (Biodex Medical Systems, Inc., Shirley, NY, USA). For all strength assessments, subjects were seated with restraining straps placed over the trunk, pelvis, and thigh and the input axis of the dynamometer was aligned with the axis of rotation of the knee. The isometric MVCs were performed at a leg angle of 30° below the horizontal plane (Conchola et al. 2013). Prior to the testing, subjects performed a 5-min warm-up on a cycle ergometer (Monark Exercise 828E, Vansbro, Sweden) at a self-selected low-intensity workload, followed by three submaximal isokinetic leg extension and leg flexion muscle actions at 60° s⁻¹ at approximately 75 % of their perceived maximal effort. Following the warm-up, subjects performed 2–3 leg flexion isometric MVCs, which were followed by three concentric and two eccentric MVCs at 60° s⁻¹ (Note: three isometric MVCs were only performed if the first two exceeded a 10 % difference of peak torque (PT) values, and two rather than three eccentric actions were performed in an attempt to minimize any potential muscle damaging effects of multiple eccentric actions). One minute of recovery time was given between each repetition and 3 min of recovery was given between each muscle action.

Experimental fatigue protocol and recovery

The highest torque value (PT, Nm) recorded from the baseline isometric MVCs (Pre) was used to determine the target torque level for the subsequent experimental fatigue protocol. The target torque level was set at 60 % of PT, as this target level has been used to invoke neuromuscular fatigue in previous investigations (Vollestad 1997; Allman and Rice 2001; Conchola et al. 2013). Participants were given a 5-min recovery period following the Pre MVCs and then performed the fatigue protocol on the Biodex dynamometer, which consisted of cyclical intermittent isometric contractions using a 0.6 duty cycle, involving a 6-s contraction followed by a 4-s relaxation phase (Bigland-Ritchie et al. 1986; Vollestad 1997; Hunter et al. 2004). During the fatigue protocol, participants were required to track their torque production by tracing a horizontal line set at the target torque level, which was displayed in real time on a computer monitor placed directly in front of them. When participants were no longer able to reach their target torque level, despite giving a maximal effort, the fatigue test was terminated. Upon termination of the fatigue protocol, two isometric and concentric MVCs and one eccentric MVC were performed at immediately (Post0), seven (Post7), fifteen (Post15), and thirty (Post30) minutes following the fatigue task (Conchola et al. 2013). Strong verbal encouragement was provided throughout the duration of the fatigue protocol, and during all MVCs (Thompson et al. 2012), and subjects were required to place their hands either on their thighs or across their torso (not being allowed to grasp the dynamometer handles or railing) to disengage any potential contribution of the upper body. In addition, in order to ensure adequate fatigue was attained for the participants, a threshold requirement of at least a 25 % reduction of isometric PT resulting from the fatigue protocol (Pre vs. Post0) was used as an inclusion criterion for the study. Consequently, only subjects that met this 25 % minimum fatigue threshold have been included in the study (two subjects failed to meet this requirement).

Signal processing and data analyses

The torque (Nm) signal was sampled at 2 KHz with a Biopac data acquisition system (MP150WSW, Biopac Systems Inc., Santa Barbara, CA, USA), stored on a personal computer (Dell Inspiron 8200, Dell Inc.,

Round Rock, TX, USA), and processed off-line with custom written software (LabVIEW 8.5, National Instruments, Austin, TX, USA). The torque signal was filtered using a fourth order, zero phase-shift, low-pass Butterworth filter with a 10 Hz cutoff frequency. For isometric muscle action analyses, the passive baseline torque value was considered the limb weight and subtracted from the signal so that the new baseline value was set at 0 Nm. Isokinetic muscle actions were also corrected for the effect of gravity on the lower leg in accordance with the gravity correction procedures described by Aagaard et al. (1995). All subsequent analyses were performed on the scaled, filtered, and gravity-corrected torque signals. Isometric PT was calculated as the highest 500 ms epoch and isokinetic PT as the highest 25 ms epoch during the respective MVC plateau. The power (W) signal was derived as the product of the torque and velocity signals, and mean power was calculated as the mean value between the power onset (determined as the point where power increased to 2 % of the maximum power value above baseline) and the maximum power value. An ECR was derived by dividing the eccentric variable (i.e., PT or mean power) by the respective concentric variable, in order to provide an index of the proportion of eccentric vs. concentric muscle function capacities. For each muscle action, the MVC with the highest PT value was selected and used for data analysis.

Statistical analyses

Two separate three-way mixed factorial analyses of variance (ANOVAs) (age group [young vs. older men] $\times$ time phase [Pre vs. Post0 vs. Post7 vs. Post15 vs. Post30] $\times$ muscle action [isometric vs. concentric vs. eccentric]) were used to analyze the PT and mean power data (only concentric and eccentric muscle actions were analyzed for mean power data). A two-way mixed factorial ANOVA (age group $\times$ time phase) was used to analyze the ECR data. When appropriate, follow-up analyses included one-way repeated measures ANOVAs and independent samples *t* tests with Bonferroni corrections on either the simple main effects (when a significant interaction was present) or main effects collapsed across the opposing variable (when no significant interaction was present). PASW software version 20.0 (SPSS Inc., Chicago, IL, USA) was used for all statistical analyses. An alpha value of $P \leq 0.05$ was considered statistically significant for all comparisons.

Results

The fatigue protocol endurance times were 274.3 ± 191.8 and 443.4 ± 364.4 s for the young and older men, respectively ($P=0.085$). Means and SD values are presented in Table 1 for all PT, mean power, and ECR variables. For PT, there was no three-way interaction (age group $\times$ time phase $\times$ muscle action; $P=0.664$), but there were two-way interactions for age group $\times$ time phase ($P=0.014$) and time phase $\times$ muscle action ($P<0.001$). For age group $\times$ time phase, PT was greater ($P<0.001$ – 0.002) for Pre compared to all other time phases for the young men but was only greater ($P<0.001$) for Pre compared to Post0 for the older men (Fig. 1a). Also, Post0 was lower ($P<0.001$) compared to all other time phases, and no differences were observed between Post7, Post15, and Post30 ($P=0.152$ – 1.000) for both the young and older men. For time phase $\times$ muscle action, PT was greater for Pre compared to all other time phases for both the isometric ($P<0.001$) and eccentric ($P<0.001$ – 0.012) muscle actions, but was only greater for Pre compared to Post0 ($P<0.001$) for the concentric muscle action (Fig. 1b). Also, Post0 was lower ($P<0.001$ – 0.009) compared to all other time phases, and no differences were observed between Post7, Post15, and Post30 ($P=0.246$ – 1.000) for all muscle actions.

For mean power, there was no three-way interaction (age group $\times$ time phase $\times$ muscle action, $P=0.275$), but there were two-way interactions for age group $\times$ time phase ($P=0.009$) and time phase $\times$ muscle action ($P<0.001$). For age group $\times$ time phase, mean power was greater ($P<0.001$) for Pre compared to all other time phases for the young men but was only greater ($P<0.001$) for Pre compared to Post0 for the older men. Also, Post0 was lower ($P<0.001$) compared to all other time phases, and no differences were observed between Post7, Post15, and Post30 ($P=1.000$) for both the young and older men. For time phase $\times$ muscle action, mean power was greater ($P<0.001$) for Pre compared to all other time phases for the eccentric muscle action, but was only greater ($P<0.001$) for Pre compared to Post0 for the concentric muscle action. Also, Post0 was lower ($P<0.001$) compared to all other time phases, and no differences were observed between Post7, Post15, and Post30 ($P=1.000$) for both the eccentric and concentric muscle actions.

For PT and mean power ECR, there was no age group $\times$ time phase interaction ($P=0.379$, 0.824), but

there were main effects for time phase ($P<0.001$). Post hoc analyses for PT ECR revealed that Pre was greater compared to Post15 ($P=0.037$) and Post30 ($P=0.001$) and Post0 was greater compared to Post7 ($P=0.019$), Post15 ($P=0.003$), and Post30 ($P=0.001$). No differences were observed between Post7, Post15, and Post30 ($P=1.000$). Post hoc analyses for mean power revealed that both Pre and Post0 were greater compared to Post7 ($P=0.020$, 0.006), Post15 ($P=0.012$, 0.001), and Post30 ($P=0.009$, 0.003) but no differences were observed between Post7, Post15, and Post30 ($P=1.000$) (Fig. 2).

Discussion

The primary findings of this investigation were that following a bout of fatigue-inducing isometric intermittent contractions, (1) older men exhibited more rapid and pronounced recovery of strength capacities than young men, and (2) concentric muscle actions recovered more rapidly than eccentric or isometric actions. Thus, the hypothesis was not supported that no age-related differences would exist in strength-based recovery characteristics; however, the prolonged recovery pattern between eccentric and isometric vs. concentric muscle actions was supported.

Age-related differences in recovery characteristics following fatiguing contractions were observed between the young and older men, when collapsed across all muscle actions. Despite a similar reduction of total PT capacity (collapsed across muscle actions) immediately following the fatigue protocol for the young (30.8 %) and older (27.6 %) men, the older men's strength levels were statistically recovered to baseline values within 7 min following fatigue (although it is notable, a residual 4.8–7.8 % reduction of PT did remain for the Post7–Post30 periods); while the young men's PT did not recover to baseline within 30 min following fatigue, exhibiting an 11.1–14.0 % reduction for the Post7–Post30 time periods (Table 1, Fig. 1a). Two previous investigations have used similar isometric intermittent fatigue protocols and recovery periods as the present study. Vollestad et al. (1997) fatigued the leg extensors of young adults (22–30 years) using a similar protocol at 60 % of MVC and reported significant reductions (12.0 % lower vs. pretest) of isometric strength capacities at ~30 min of recovery—which matches the 11.1 % reduction of PT at 30 min for the young in the present study. Allman and Rice (2001) also used a similar

Table 1 Mean (SD) values for peak torque, mean power, and eccentric/concentric ratio (ECR) variables for all muscle actions and time phases in young and old men

Variable	Young Men						Old Men					
	Pre	Post0	Post7	Post15	Post30		Pre	Post0	Post7	Post15	Post30	
Peak Torque (Nm)	127.75 (19.59)	79.23 (11.19)	108.93 (21.30)	111.22 (19.04)	115.31 (24.85)		97.62 (14.65)	60.16 (9.00)	84.81 (11.98)	90.18 (12.25)	87.37 (14.36)	
	123.54 (24.33)	86.95 (29.10)	111.58 (25.66)	113.81 (24.11)	117.31 (24.47)		91.59 (13.59)	68.41 (10.83)	90.60 (14.34)	92.19 (13.70)	90.12 (15.51)	
	147.74 (43.68)	110.05 (34.91)	122.50 (38.09)	122.02 (38.38)	122.32 (35.68)		110.33 (18.73)	88.24 (22.35)	101.93 (19.60)	102.88 (21.89)	98.57 (23.04)	
Mean Peak Torque [†]	133.02 ^a (29.20)	92.08 [*] (25.07)	114.35 ^{*a} (28.35)	115.69 ^{*a} (27.18)	118.32 ^{*a} (28.33)		99.85 ^a (15.66)	72.28 [*] (14.06)	92.45 ^a (15.31)	95.09 ^a (15.95)	92.03 ^a (17.64)	
Mean Power (W)	92.92 (20.91)	55.16 (21.41)	77.33 (19.53)	80.93 (18.50)	80.26 (20.15)		65.80 (8.81)	43.24 (10.75)	67.87 (12.53)	65.40 (11.58)	64.57 (11.25)	
	113.07 (25.59)	76.13 (24.31)	92.19 (26.53)	125.14 (23.06)	92.78 (25.06)		87.17 (14.89)	60.26 (15.00)	73.51 (13.40)	74.16 (14.39)	72.59 (16.07)	
	103.00 ^a (23.25)	65.65 [*] (22.86)	84.77 ^{*a} (23.03)	86.06 ^{*a} (20.78)	86.53 ^{*a} (22.61)		75.54 ^a (11.85)	50.89 [*] (12.88)	70.10 ^a (12.97)	69.84 ^a (12.99)	67.98 ^a (13.66)	
ECR	1.18 (0.20)	1.32 (0.48)	1.09 ^c (0.20)	1.06 ^{bc} (0.20)	1.04 ^{bc} (0.21)		1.21 (0.22)	1.30 (0.34)	1.13 ^c (0.19)	1.11 ^{bc} (0.20)	1.09 ^{bc} (0.17)	
	1.23 (0.17)	1.45 (0.45)	1.20 ^{bc} (0.21)	1.14 ^{bc} (0.22)	1.17 ^{bc} (0.24)		1.33 (0.23)	1.47 (0.55)	1.11 ^{bc} (0.24)	1.14 ^{bc} (0.19)	1.13 ^{bc} (0.20)	

Shaded block indicates significant time phase × muscle action interaction (collapsed across age group) where shaded region is significantly different compared to Pre

*Significant difference compared to pre

†Significant age group × time phase interaction (collapsed across muscle action)

^aSignificant difference compared to Post0

^bSignificant difference compared to Pre collapsed across age group

^cSignificant difference compared to Post0 collapsed across age group. $P \leq 0.05$

Fig. 1 Peak torque (PT) values for the **a** young and older men and **b** isometric, eccentric, and concentric muscle actions across time phases. *Dagger* indicates an interaction for **a** showing that all Post time phases were lower compared to Pre for the young men but only Post0 was lower than Pre for the older men (collapsed across muscle actions) and **b** showing that all Post time phases were lower compared to Pre for the isometric and eccentric muscle actions but only Post0 was lower than Pre for the concentric muscle action (collapsed across age group). *Asterisk* indicates significantly lower compared to Pre. Values are mean+SEM. Numbers inside figure are percentage values of Pre (concentric values omitted for clarity)

fatigue protocol, but examined the forearm flexors, in which they compared fatigue and recovery characteristics between young and older men. These authors reported no age-related differences in recovery of strength capacities up to 60 min post-fatigue, showing that MVC force levels were significantly reduced by 10.0 % at 30 min of recovery in both age groups. These findings specifically corroborate the isometric muscle action findings of the present study, but diverge from the present results when collapsed across muscle actions (decreased PT of only 7.8 % for the older, but 14.7 % for the young men). This apparent disparity is largely a function of the more rapid recovery of concentric PT for

Fig. 2 Eccentric/concentric ratio (ECR) values for mean power showing Post7, Post15, and Post30 were lower compared to both Pre and Post0 time phases (collapsed across age group). Values are mean+SEM. *Asterisk* indicates significantly different from both Pre and Post0. Numbers inside figure are percentage values of Pre the older men, which was not large enough to yield a significant three-way interaction, but nevertheless had enough leverage to lower the magnitude of the reduction of PT at 30 min recovery in the older age group when collapsed across the other two muscle actions. Thus, although Allman and Rice (2001) concluded no effects of age on recovery of isometric strength responses from fatigue, based on our analyses, we must conclude the contrary for combined dynamic and isometric muscle actions, which favors more rapid recovery in older men.

Plausible mechanisms for these findings are likely not related to neuromuscular activation impairments, as previous evidence suggests that age-related responses to muscle fatigue are unlikely to be attributed to either peripheral or central activation differences between healthy young and older adults as a result of moderate to high intensity intermittent isometric fatiguing contractions (Allman and Rice 2001; Kent-Braun et al. 2002; Lanza et al. 2004; Chung et al. 2007; Callahan et al. 2009). Alternatively, the observed force reducing fatigue responses are more likely to reside within the muscle, with fatigue accumulation resulting from intramuscular metabolic changes (Miller et al. 1995; Vollestad et al. 1997; Allen and Westerblad 2001; Allman and Rice 2001), and excitation contraction coupling (ECC) impairments (Baker et al. 1993; Jones 1996). Changes in metabolites leading to phosphocreatine (PCr) depletion, and accumulation of H^+ , inorganic phosphate (P_i), and deprotonated inorganic phosphate ($H_2PO_4^-$), have been associated with fatigue-related processes on cellular mechanisms controlling force production (Miller et al. 1995; Allen and Westerblad 2001). Some evidence suggests that older individuals may

exhibit less fatigue-related metabolic perturbations, such as smaller decreases in intracellular pH and PCr, and accumulate less P_i and $H_2PO_4^-$ compared to young adults (Kent-Braun et al. 2002; Lanza et al. 2005, 2007). One explanation of the divergent age-related recovery responses may be related to the differential effects of age on increases in P_i and Ca^{2+} concentrations during repetitive forceful contractions. Rising levels of P_i during muscular contraction, a consequence of substrate utilization, have been shown to reduce depolarization-induced Ca^{2+} release from the sarcoplasmic reticulum, thus, limiting force production (Dutka et al. 2005; Posterino and Dunn 2008). Previous studies (Kent-Braun et al. 2002; Lanza et al. 2007) have shown lower increases of intracellular concentrations of P_i and $H_2PO_4^-$ during exercise in older compared to young subjects, which may be a result of greater reliance on oxidative ATP sources in the older adults yielding less metabolite accumulation (Kent-Braun et al. 2002; Lanza et al. 2005, 2007). Age-related muscle fiber transformation from Type II to Type I (Lexell 1995; Lee et al. 2006) with advanced age may also play a role in mitigating the effects of fatigue responses on subsequent recovery patterns. For example, under conditions of contraction, Type II fibers have been shown to exhibit more depressed contractility with the presence of P_i (Posterino and Dunn 2008) and ADP (Macdonald and Stephenson 2006); greater contraction-induced SR function/ Ca^{2+} release impairments (Li et al. 2002) and lowered Ca^{2+} sensitivity (Hvid et al. 2013) and release 3–4-fold greater amounts of Ca^{2+} per comparable stimuli (Baylor and Hollingworth 2012) when compared to Type I fibers. Moreover, these fiber type attributes may contribute to the higher susceptibility of Type II fibers to low frequency fatigue (Powers and Binder 1991; Rijkkelijkhuizen et al. 2003), which is supported in terms of age-specific effects on low frequency fatigue by the findings of Bilodeau et al. (2001) who showed greater low frequency fatigue in young vs. older subjects in the time period following fatiguing contractions of the elbow flexors. Notably, it appears to be the elevation of intracellular Ca^{2+} concentration (more specifically the Ca^{2+} -time integral) throughout the exercise that plays a primary role in the development of low frequency fatigue several minutes into the recovery period (Chin and Allen 1996; Chin et al. 1997), likely due to the disruption of ECC processes caused by Ca^{2+} -activated proteases/lipases (Bruton et al. 1998; Verburg et al. 2005). One hypothesis we propose may be that the

excitation contraction uncoupling reported in older adults (Delbono et al. 1995; Boncompagni et al. 2006), may be advantageous for reducing contraction-induced intracellular Ca^{2+} levels (particularly the Ca^{2+} -time integral) during exercise, which would consequently attenuate the magnitude of low frequency fatigue. Together, the changes with aging that yield lower ECC and metabolite accumulation during muscular contraction, fiber type changes, and lower motor unit discharge rates may produce a scenario which provides (despite the unfavorable effects on absolute force production capacities) reduced levels of intracellular Ca^{2+} , and thereby diminishing subsequent deleterious effects of high Ca^{2+} levels on the development of low frequency fatigue. Although the present findings would seem to support this hypothesis, a limitation of this study was the inability to identify any of the mechanisms that may be associated with these findings. It is also notable that, as expected, the peak torque of the young men was substantially higher than the older men which yielded greater absolute torque output performance during the fatigue protocol. Although the level of post-fatigue strength decrements was standardized across both groups, it is plausible that the inherent age-related strength differences may also have played a role in the present recovery differences. Finally, the effects of learning on the fatigue protocol and testing procedures may have impacted the outcome measures, although the longer fatigue endurance times for the older men (443.4 s) compared to the young men (274.3 s) would seem to suggest the effects of impaired learning on these procedures by the older group were not present or at a minimum. The disparity in endurance times which favors the older adults is notable, especially when coupled with the findings of the older group's enhanced recovery from the effects of the protocol. Although many of the physiological mechanisms mentioned above may provide a rationale for this phenomenon (i.e., age-related fiber type transformation, enhanced contractile efficiency, excitation contraction uncoupling etc. for older adults), future studies in which multiple recovery assessments are taken, in conjunction with a standardized level of fatigue induction across age groups, would help to validate and elucidate the nature of these responses. Specifically, further research is needed examining the age-related effects of acute recovery responses following contraction-induced fatigue which utilizes more sophisticated physiological assessments (contractile properties, muscle biopsies, motor unit decomposition, etc.)

aimed at elucidating the specific mechanisms responsible for any observed divergence of recovery patterns as a result of aging.

A novel finding of the present study was the more rapid and pronounced recovery of the concentric PT and power compared to the isometric and eccentric muscle actions, which was not influenced by age. Concentric PT and power were recovered to baseline levels at 7 min post exercise, whereas both the eccentric and isometric muscle actions exhibited depressed PT and power for up to 30 min into recovery (10.1–17.4 % lower at 30 min vs. pretest). It is possible that differences in neural activation strategies between muscle actions may be the basis for these findings. When compared to concentric muscle actions, a number of authors have reported eccentric actions exhibit reduced muscle activation (Enoka 1996; Del Valle and Thomas 2005), lower motor unit discharge rates (Enoka 1996; Del Valle and Thomas 2005; Kallio et al. 2013), selective activation of high-threshold motor units (Nardone et al. 1989; Enoka 1996), and lower motor-evoked potential area and Hoffman reflex amplitude (Enoka 1996). A lower magnitude of activation as well as discharge rates during eccentric actions may lead to more pronounced force decrements in the presence of low frequency fatigue because it is characterized by force reductions specifically at lower frequencies. This would have substantial effects on force production given that the lower frequencies for eccentric actions may likely fall on the steep portion of the force-frequency curve, such that small changes in discharge frequency may have relatively large impacts on force production. Also, the selective activation of high-threshold motor units during eccentric actions may more preferentially impair eccentric force production during low frequency fatigue because it is the fibers associated with these motor units (Type II) that may undergo greater exercise-induced low frequency fatigue compared to Type I (Powers and Binder 1991; Rijkkelijkhuizen et al. 2003). These combined effects were reflected in the ECR (Fig. 2) which demonstrated a brief increase at post exercise but then declined significantly to below baseline values for the duration of the 30-min recovery period. This reduction was likely a function of the development of low frequency fatigue (see above), and this ratio may thus be a useful indicator of recovery status from fatigue. Importantly, the proportionally greater reduction of eccentric muscle performance characterized by slower recovery following exercise may have detrimental impact on injury risks, as

well as functional performances during this period of “supposed” recovery. Eccentric actions occur frequently in daily activities and athletic performance as well as serve to attenuate impact forces and protect less compliant structures during braking movements (Enoka 1996). The greater exercise-induced depression of force capacities for the eccentric actions across a 30-min recovery period shown in the present study is suggestive of a relatively extended period of time whereby physical activities may be compromised in terms of both optimal performance as well as potential for injury as a result of low eccentric force production abilities. This finding appears to be particularly useful in the context of this study for the reason that these depressed strength responses were demonstrated for the eccentric actions specifically for the hamstrings muscles, which is a key contributing muscle group toward injury risk profiling (specifically to the functional eccentric hamstrings to concentric quadriceps ratio) (Jenkins et al. 2013), as well as being a sensitive muscle group for identifying/discriminating both athletic (Jenkins et al. 2013; Thompson et al. 2013) and clinical-based functional status (Bento et al. 2010; Palmer et al. 2014).

In summary, strength- and power-related recovery responses subsequent to induced fatigue of the leg flexors may be augmented in older vs. younger men for various types of muscle actions, and this may be a result of physiological changes occurring at advanced age. The higher force producing muscle actions, which include both eccentric and isometric actions, recovered slower from fatigue compared to concentric actions, and this was reflected by the ECR and was also independent of age. In practice, greater exercise-induced reductions of eccentric strength and power for extended durations of recovery may unfavorably impact the hamstrings to quadriceps performance ratio, and thereby lead to increased injury risks and performance deficits. Such a scenario may be present even when coaches or clinicians may perceive the effects of fatigue to be fully restored, such as following a several-minute rest period. Caution may be prudent in scenarios involving training, rehabilitation, or other settings where physical activity-induced fatigue has resulted from moderately-high intensity, intermittent exercise/activity patterns in which further physical activity is required given the possibility of proportionally higher strength-based impairments in activities consisting of a functional eccentric component (i.e., explosive- or strength-based tasks, balance, reaction time, etc.). Interestingly, the potential ramifications

of reduced strength-based performance abilities during short-term periods of recovery from fatigue may be more paramount for younger than for older adults.

Compliance with ethical standards

Informed consent All participants completed and signed an informed consent document and health history questionnaire prior to any testing.

References

- Aagaard P, Simonsen EB, Trolle M, Bangsbo J, Klausen K (1995) Isokinetic hamstring/quadriceps strength ratio: influence from joint angular velocity, gravity correction and contraction mode. *Acta Physiol Scand* 154:421–427
- Allen DG, Westerblad H (2001) Role of phosphate and calcium stores in muscle fatigue. *J Physiol* 536:657–665
- Allman BL, Rice CL (2001) Incomplete recovery of voluntary isometric force after fatigue is not affected by old age. *Muscle Nerve* 24:1156–1167
- Baker AJ, Kostov KG, Miller RG, Weiner MW (1993) Slow force recovery after long-duration exercise: metabolic and activation factors in muscle fatigue. *J Appl Physiol* (1985) 74: 2294–2300
- Baylor SM, Hollingworth S (2012) Intracellular calcium movements during excitation-contraction coupling in mammalian slow-twitch and fast-twitch muscle fibers. *J Gen Physiol* 139: 261–272
- Bennett JG, Stauber WT (1986) Evaluation and treatment of anterior knee pain using eccentric exercise. *Med Sci Sports Exerc* 18:526–530
- Bento PC, Pereira G, Ugrinowitsch C, Rodacki AL (2010) Peak torque and rate of torque development in elderly with and without fall history. *Clin Biomech (Bristol, Avon)* 25:450–454
- Bigland-Ritchie B, Cafarelli E, Vollestad NK (1986) Fatigue of submaximal static contractions. *Acta Physiol Scand Suppl* 556:137–148
- Bilodeau M, Erb MD, Nichols JM, Joiner KL, Weeks JB (2001) Fatigue of elbow flexor muscles in younger and older adults. *Muscle Nerve* 24:98–106
- Boncompagni S, d'Amelio L, Fulle S, Fano G, Protasi F (2006) Progressive disorganization of the excitation-contraction coupling apparatus in aging human skeletal muscle as revealed by electron microscopy: a possible role in the decline of muscle performance. *J Gerontol A Biol Sci Med Sci* 61: 995–1008
- Bruton JD, Lannergren J, Westerblad H (1998) Mechanisms underlying the slow recovery of force after fatigue: importance of intracellular calcium. *Acta Physiol Scand* 162:285–293
- Callahan DM, Foulis SA, Kent-Braun JA (2009) Age-related fatigue resistance in the knee extensor muscles is specific to contraction mode. *Muscle Nerve* 39:692–702
- Chin ER, Allen DG (1996) The role of elevations in intracellular $[Ca^{2+}]$ in the development of low frequency fatigue in mouse single muscle fibres. *J Physiol* 491(Pt 3):813–824
- Chin ER, Balnave CD, Allen DG (1997) Role of intracellular calcium and metabolites in low-frequency fatigue of mouse skeletal muscle. *Am J Physiol* 272:C550–C559
- Christie A, Snook EM, Kent-Braun JA (2011) Systematic review and meta-analysis of skeletal muscle fatigue in old age. *Med Sci Sports Exerc* 43:568–577
- Chung LH, Callahan DM, Kent-Braun JA (2007) Age-related resistance to skeletal muscle fatigue is preserved during ischemia. *J Appl Physiol* 103:1628–1635
- Conchola EC, Thompson BJ, Smith DB (2013) Effects of neuromuscular fatigue on the electromechanical delay of the leg extensors and flexors in young and old men. *Eur J Appl Physiol* 113:2391–2399
- Del Valle A, Thomas CK (2005) Firing rates of motor units during strong dynamic contractions. *Muscle Nerve* 32:316–325
- Delbono O, O'Rourke KS, Ettinger WH (1995) Excitation-calcium release uncoupling in aged single human skeletal muscle fibers. *J Membr Biol* 148:211–222
- Deschenes MR (2011) Motor unit and neuromuscular junction remodeling with aging. *Curr Aging Sci* 4:209–220
- Dutka TL, Cole L, Lamb GD (2005) Calcium phosphate precipitation in the sarcoplasmic reticulum reduces action potential-mediated Ca^{2+} release in mammalian skeletal muscle. *Am J Physiol Cell Physiol* 289:C1502–C1512
- Enoka RM (1996) Eccentric contractions require unique activation strategies by the nervous system. *J Appl Physiol* (1985) 81: 2339–2346
- Gray JC, Chandler JM (1989) Percent decline in peak torque production during repeated concentric and eccentric contractions of the quadriceps femoris muscle. *J Orthop Sports Phys Ther* 10:309–314
- Greig M (2008) The influence of soccer-specific fatigue on peak isokinetic torque production of the knee flexors and extensors. *Am J Sports Med* 36:1403–1409
- Hortobagyi T, Zheng D, Weidner M, Lambert NJ, Westbrook S, Houmard JA (1995) The influence of aging on muscle strength and muscle fiber characteristics with special reference to eccentric strength. *J Gerontol A Biol Sci Med Sci* 50: B399–B406
- Hunter SK, Duchateau J, Enoka RM (2004) Muscle fatigue and the mechanisms of task failure. *Exerc Sport Sci Rev* 32:44–49
- Hvid LG, Gejl K, Bech RD, Nygaard T, Jensen K, Frandsen U, Ortenblad N (2013) Transient impairments in single muscle fibre contractile function after prolonged cycling in elite endurance athletes. *Acta Physiol (Oxf)* 208:265–273
- Iguchi M, Shields RK (2010) Quadriceps low-frequency fatigue and muscle pain are contraction-type-dependent. *Muscle Nerve* 42:230–238
- Jenkins ND, Hawkey MJ, Costa PB, Fiddler RE, Thompson BJ, Ryan ED, Smith D, Sobolewski EJ, Conchola EC, Akehi K, Cramer JT (2013) Functional hamstrings: quadriceps ratios in elite women's soccer players. *J Sports Sci* 31:612–617
- Jones DA (1996) High-and low-frequency fatigue revisited. *Acta Physiol Scand* 156:265–270
- Kallio J, Sogaard K, Avela J, Komi PV, Selanne H, Linnamo V (2013) Motor unit firing behaviour of soleus muscle in isometric and dynamic contractions. *PLoS One* 8, e53425

- Kamen G, Sison SV, Du CC, Patten C (1995) Motor unit discharge behavior in older adults during maximal-effort contractions. *J Appl Physiol* (1985) 79:1908–1913
- Kent-Braun JA (2009) Skeletal muscle fatigue in old age: whose advantage? *Exerc Sport Sci Rev* 37:3–9
- Kent-Braun JA, Ng AV, Doyle JW, Towse TF (2002) Human skeletal muscle responses vary with age and gender during fatigue due to incremental isometric exercise. *J Appl Physiol* 93:1813–1823
- Lanza IR, Russ DW, Kent-Braun JA (2004) Age-related enhancement of fatigue resistance is evident in men during both isometric and dynamic tasks. *J Appl Physiol* 97:967–975
- Lanza IR, Befroy DE, Kent-Braun JA (2005) Age-related changes in ATP-producing pathways in human skeletal muscle in vivo. *J Appl Physiol* (1985) 99:1736–1744
- Lanza IR, Larsen RG, Kent-Braun JA (2007) Effects of old age on human skeletal muscle energetics during fatiguing contractions with and without blood flow. *J Physiol* 583:1093–1105
- Lee WS, Cheung WH, Qin L, Tang N, Leung KS (2006) Age-associated decrease of type IIA/B human skeletal muscle fibers. *Clin Orthop Relat Res* 450:231–237
- Lexell J (1995) Human aging, muscle mass, and fiber-type composition. *J Gerontol A-Biol Sci Med Sci* 50:11–16
- Li JL, Wang XN, Fraser SF, Carey MF, Wrigley TV, McKenna MJ (2002) Effects of fatigue and training on sarcoplasmic reticulum Ca^{2+} regulation in human skeletal muscle. *J Appl Physiol* (1985) 92:912–922
- Macdonald WA, Stephenson DG (2006) Effect of ADP on slow-twitch muscle fibres of the rat: implications for muscle fatigue. *J Physiol* 573:187–198
- Marshall PW, Mannion J, Murphy BA (2010) The eccentric, concentric strength relationship of the hamstring muscles in chronic low back pain. *J Electromyogr Kinesiol* 20:39–45
- Miller RG, Kent-Braun JA, Sharma KR, Weiner MW (1995) Mechanisms of human muscle fatigue. Quantitating the contribution of metabolic factors and activation impairment. *Adv Exp Med Biol* 384:195–210
- Nardone A, Romano C, Schieppati M (1989) Selective recruitment of high-threshold human motor units during voluntary isometric lengthening of active muscles. *J Physiol* 409:451–471
- Palmer TB, Thiele RM, Williams KB, Adams BM, Akehi K, Smith DB, Thompson BJ (2014) The identification of fall history using maximal and rapid isometric torque characteristics of the hip extensors in healthy, recreationally active elderly females: a preliminary investigation. *Aging Clin Exp Res*
- Posterino GS, Dunn SL (2008) Comparison of the effects of inorganic phosphate on caffeine-induced Ca^{2+} release in fast- and slow-twitch mammalian skeletal muscle. *Am J Physiol Cell Physiol* 294:C97–C105
- Powers RK, Binder MD (1991) Effects of low-frequency stimulation on the tension-frequency relations of fast-twitch motor units in the cat. *J Neurophysiol* 66:905–918
- Rijkkelijhuizen JM, de Ruiter CJ, Huijing PA, de Haan A (2003) Low-frequency fatigue is fibre type related and most pronounced after eccentric activity in rat medial gastrocnemius muscle. *Pflugers Arch* 447:239–246
- Small K, McNaughton L, Greig M, Lovell R (2010) The effects of multidirectional soccer-specific fatigue on markers of hamstring injury risk. *J Sci Med Sport* 13:120–125
- Smith IC, Newham DJ (2007) Fatigue and functional performance of human biceps muscle following concentric or eccentric contractions. *J Appl Physiol* (1985) 102:207–213
- Tesch PA, Dudley GA, Duvoisin MR, Hather BM, Harris RT (1990) Force and EMG signal patterns during repeated bouts of concentric or eccentric muscle actions. *Acta Physiol Scand* 138:263–271
- Thompson BJ, Ryan ED, Herda TJ, Costa PB, Walter AA, Sobolewski EJ, Cramer JT (2012) Consistency of rapid muscle force characteristics: influence of muscle contraction onset detection methodology. *J Electromyogr Kinesiol* 22: 893–900
- Thompson BJ, Ryan ED, Sobolewski EJ, Smith DB, Conchola EC, Akehi K, Buckminster T (2013) Can maximal and rapid isometric torque characteristics predict playing level in division I American collegiate football players? *J Strength Cond Res* 27:655–661
- Verburg E, Murphy RM, Stephenson DG, Lamb GD (2005) Disruption of excitation-contraction coupling and titin by endogenous Ca^{2+} -activated proteases in toad muscle fibres. *J Physiol* 564:775–790
- Vollestad NK (1997) Measurement of human muscle fatigue. *J Neurosci Methods* 74:219–227
- Vollestad NK, Sejersted I, Saugen E (1997) Mechanical behavior of skeletal muscle during intermittent voluntary isometric contractions in humans. *J Appl Physiol* (1985) 83:1557–1565
- Westblad P, Tsai-Fellander L, Johansson C (1995) Eccentric and concentric knee extensor muscle performance in professional ballet dancers. *Clin J Sport Med* 5:48–52