ABSTRACT: In this investigation we examined age-associated changes in peak torque, voluntary activation levels, and potentiated twitch properties of the knee extensors during isometric (ISO), shortening (SHO), and lengthening (LEN) actions in 18 young subjects (19–27 years) and 12 elderly subjects (64–77 years). Peak torque was lower for the elderly subjects under the ISO (−31%) and SHO (−28%) conditions ($P < 0.05$); however, the loss in LEN peak torque in the elderly was less marked (−17%) ($P > 0.05$). Voluntary activation levels within and between groups were not significantly different and ranged between 96.8% and 98.9% ($P > 0.05$). Peak twitch torque and some temporal twitch characteristics were altered with age ($P < 0.05$), but such changes were similar across all muscle actions ($P > 0.05$). These data suggest that the attenuated reduction in LEN muscle strength associated with age is probably not related to contraction-specific changes in voluntary activation levels or potentiated twitch properties.
Muscle Nerve **39:** 683–691, 2009

EFFECT OF AGE ON MUSCLE ACTIVATION AND TWITCH PROPERTIES DURING STATIC AND DYNAMIC ACTIONS

MELISSA R. WILDER, BExSc(Hons), and JACK CANNON, PhD

Exercise and Sports Science Laboratories, School of Human Movement Studies,
Charles Sturt University, Building N1, Panorama Avenue, Bathurst, New South Wales 2795, Australia

Accepted 21 October 2008

Losses in muscle strength with age appear to occur at a steady rate of approximately 1–2% per year between the sixth and eighth decades. These losses accelerate thereafter and ultimately result in reductions of 15–40% between 20–30 years and 65–80 years of age.[32] Interestingly, evidence indicates the extent of the age-associated reduction in muscle strength is contraction-type-dependent, and reductions in strength with age appear to be attenuated during lengthening (LEN) actions compared with isometric (ISO) or shortening (SHO) efforts.[5] The attenuated reduction in muscle strength with age during LEN actions compared with ISO and SHO conditions appears to be a stable and enduring phenomenon that is independent of advanced age, gender, muscle group, or the velocity of contraction.[5,23,24,30]

The neuromuscular mechanisms responsible for the less marked reduction in LEN muscle strength with age have yet to be fully elucidated. One possible contributing factor is an age-associated change in voluntary activation.[8,29] Voluntary activation can be influenced by a number of factors, including the level of descending motor drive and the excitability and/or inhibition of cortical and spinal motor neurons.[17] Interestingly, Earles et al.[7] reported age-associated differences in the regulation of motor unit output. ISO forces in young men were primarily maintained through modulating presynaptic inhibition, whereas elderly men were more reliant on volitional motor unit activation. Previous studies on age-associated changes in voluntary activation have examined ISO muscle actions and provided conflicting results.[10,16,34] However, investigations comparing age-associated changes in voluntary activation between ISO, SHO, and LEN actions are limited.[17,35] This is surprising given that the results obtained under ISO conditions do not represent the type of muscle activity used during daily activities. In addition, age-related changes in the rate of contraction may also contribute to the relative maintenance of LEN muscle strength with age by providing greater resistance to active muscle lengthening due to the mechanical disruption of actomyosin cross-bridges.[29,30] As such, assessing evoked twitch contractile properties may provide a model of contractile behavior that provides insight into the contribution of altered contractile function to the less marked re-

Abbreviations: ½RT; half-relaxation time; ANOVA, analysis of variance; CD, contraction duration; ISO, isometric action; LEN; lengthening action; Pt, potentiated peak twitch torque; PT, voluntary peak torque; RR; rate of relaxation; RTD, rate of torque development; SHO, shortening action; TPt, time to peak potentiated twitch torque

Key words: aging; eccentric; knee extensors; voluntary activation; twitch contractile properties

Correspondence to: J. Cannon; e-mail: jcannon@csu.edu.au

Published online 21 January 2009 in Wiley InterScience (www.interscience.wiley.com). DOI 10.1002/mus.21233

duction in LEN muscle strength with age. Yet, despite the value of such an investigation, no available studies have compared age-related changes in evoked twitch contractile properties between muscle actions.

The purpose of the present study was to compare voluntary peak torque, voluntary activation levels, and potentiated twitch contractile properties of the knee extensors between young and elderly subjects during ISO, SHO, and LEN muscle actions. We examined evoked twitch responses in the potentiated state (as opposed to a resting twitch response) to evaluate muscle contractile behavior. Postactivation potentiation refers to the increase in peak twitch torque and rate of contraction and relaxation observed when the evoked assessment is preceded by a maximal voluntary contraction.[1,3] In this way, the model of contractile behavior used in the present study may more likely represent the functional characteristics of active muscle.

METHODS

Subject Sample. Eighteen young subjects (11 men and 7 women) and 12 elderly subjects (6 men and 6 women) volunteered to participate in this study. Physical characteristics for the young subjects were: age range, 19–27 years; mean age, 22.9 ± 4.3 years; height, 174.2 ± 10.7 cm; mass, 76.3 ± 14.1 kg; and body mass index, 25.2 ± 4.3. Physical characteristics for the elderly subjects were: age range, 64–77 years; mean age, 69.3 ± 3.7 years; height, 165.8 ± 8.9 cm; mass, 78.6 ± 17.9 kg; and body mass index, 28.4 ± 4.8. None of the subjects had ever been diagnosed with a medical condition nor had they been taking any prescribed medication thought likely to influence the results of the study (e.g., angiotensin-converting enzyme inhibitors), and were asymptomatic following the completion of a health assessment questionnaire. All subjects were non-smokers and moderately active, regularly participating in various moderate-intensity recreational activities 2–3 days per week, such as walking and golf. None of the subjects had any background in regular resistance or endurance training or competitive sports prior to the study. Subjects were informed of the purpose and design of the investigation, and written consent was obtained after subjects had the opportunity to experience the testing procedures. The investigation was conducted with the approval of the ethics in human research committee of Charles Sturt University. A familiarization session was conducted approximately 1 week prior to testing, and no subject reported any subsequent muscle soreness.

Data Collection Apparatus. All tests were performed using a Kin-Com isokinetic dynamometer (Model 125H; Chattanooga Group, Inc., Hixon, Tennessee) linked to a BNC2100 terminal block connected to a signal acquisition system (PXI1024; National Instruments, Austin, Texas), which performed A/D conversion at 16-bit resolution and synchronously sampled all data at a rate of 1 kHz. Muscle activation was achieved using two 90 × 50 mm reusable self-adhesive gel pad electrodes (Verity Medical, Ltd., Stockbridge, Hampshire, UK). With the knee positioned at 65° flexion (0° being full extension), the anode was positioned medially on the anterior aspect of the upper thigh ∽2 cm directly below the inguinal fold, and the cathode electrode was positioned medially on the anterior aspect of the lower thigh ∽5 cm above the superior border of the patella. The current applied was delivered by a constant-current stimulator (DS7AH; Digitimer; Welwyn Garden City, Hertfordshire, UK) linked to a BNC2100 terminal block connected to a signal acquisition system (PXI1024; National Instruments) using a single square-wave pulse with a width of 200 μs (400 V with a current of 250–480 mA), which was driven using customized software (version 8.0, LabView; National Instruments). Initially, the current was applied in incremental steps until the twitch amplitude plateaued. The current was then increased by a further 25% to ensure supramaximal stimulation of the intramuscular nerve branches and was used for all tests.

Subject Positioning and Warm-Up. Subjects were seated upright on the dynamometer with the hip at an angle of 100° flexion (0° being full extension) and secured via a waist strap. During all tests, subjects positioned their arms across their chest to ensure that additional forces did not contribute to performance. The axis of rotation of the dynamometer was aligned with the lateral epicondyle of the femur with the lower leg attached to the lever arm 1 cm above the lateral malleolus of the ankle. Once positioned, subjects performed a standardized warm-up, which consisted of a series of ISO knee extensions at 65° flexion (0° being full extension). Specifically, the warm-up involved: (1) four contractions at ∽50% maximal effort (5-s rest between efforts); (2) two contractions at ∽75% maximal effort (10-s rest between efforts) followed by 10-s rest; (3) two contractions at ∽90% maximal effort (20 s rest between efforts) followed by 10-s rest; and (4) one contraction at ∽100% maximal effort. A rest period of 2 min elapsed prior to the commencement of testing.

Superimposed Maximal Voluntary Contractions and Potentiated Twitch Contractions. Testing consisted of a series of at least six trials under ISO, SHO, and LEN conditions, which were performed in random order. For the ISO condition, testing was performed at 65° knee flexion (0° being full extension), which is the optimal angle for the knee extensor peak ISO torque in both young and elderly individuals.[25] For superimposed testing, subjects were instructed to produce maximal effort as fast as possible and to continue exerting maximal effort until instructed to relax, which was typically within 3–4 s. During each ISO trial, the trigger for stimulation was manually primed within 1–2 s after initiation of each contraction. Once primed, the stimulus was automatically triggered when customized software detected a decline in peak force (version 8.0, LabView; National Instruments). Manual priming of the trigger was necessary to prevent premature stimulation prior to the attainment of peak force. When primed, the decline in peak force necessary to automatically trigger the stimulus was $<1\%$. Within 5 s following each ISO superimposed contraction, a second stimulus was delivered with the muscle at complete rest.

For SHO and LEN conditions, testing was performed within a range of 15° to 80° knee flexion (0° being full extension) at a velocity of 25°/s (0.44 rad/s). This velocity is comparable with that used in previous studies assessing evoked twitch properties and voluntary activation levels under dynamic conditions.[9,17,35] During dynamic testing, subjects were instructed to produce maximal effort as fast as possible and continue exerting maximal effort throughout the full range of motion with the stimulus triggered automatically as the knee passed through 65° flexion (0° being full extension). Immediately following the SHO and/or LEN superimposed contractions, subjects were instructed to fully relax, after which the lower limb was passively moved through the same range of motion and at the same velocity for a series of ten repetitions under SHO and LEN conditions. The first six passive movements were used to determine the viscoelastic and gravitational forces that act on the lower leg during dynamic testing. During the final four passive movements under SHO and LEN conditions, the stimulus was automatically triggered by customized software (version 8.0, LabView) as the knee passed through 65° flexion (0° being full extension). A minimum of 30-s rest elapsed between each trial, and a minimum period of 5 min elapsed between conditions. Strong verbal encouragement was provided during all voluntary efforts, and subjects received continual visual feedback of performance from a computer monitor.

Data Processing and Analysis. *Gravity Correction.* All data were processed offline using spreadsheet software for Windows (Excel 2007; Microsoft Corp., Redmond, Washington). Force and knee position data were recorded to four decimal places. For the ISO condition, correction for the effect of gravity on the lower leg during the superimposed and passive evoked contractions was performed by calculating the average load applied to the force transducer during the 50-ms period immediately prior to force onset. The average load applied to the transducer during this period was used to offset force data. For the dynamic conditions, correction for the effect of gravity and viscoelastic forces on the lower leg during each superimposed and passive evoked contraction were performed by offsetting the force applied to the transducer at each angular position throughout the full range of motion during testing by the average force applied to the transducer at each angular position during the passive movements with the muscle at complete rest. Once corrected for the effect of gravity and/or viscoelastic forces on the lower leg, force data were then multiplied by lever arm length and expressed in units of torque (N · m).

Voluntary Activation Levels. Voluntary activation levels were calculated using the twitch interpolation technique. For the ISO condition, peak superimposed torque following the delivery of the stimulus was determined as the peak ISO torque value produced during the 50–150-ms period subsequent to the delivery of the stimulus. Voluntary peak torque during each superimposed contraction was determined as the mean torque value produced during the 25 ms prior to the delivery of the stimulus. Interpolated twitch torque was subsequently determined as ISO peak superimposed torque minus ISO voluntary peak torque and was calculated to four decimal places (Fig. 1).

During the dynamic contractions, peak superimposed torque following the delivery of the stimulus was determined as the peak torque value produced during the 50–150-ms period subsequent to the delivery of the stimulus. Because an ascending–descending torque–angle relationship was observed for the SHO and LEN conditions (due to changes in muscle and moment arm length, and the level of activation), it was necessary to estimate voluntary peak torque at the same joint angle at which peak superimposed torque was attained. This was performed by linear extrapolation of the torque data from the 50 data points prior to delivery of the stimulus beyond the point at which peak superimposed torque was attained (typically 20 data points), where voluntary peak torque was predicted at the

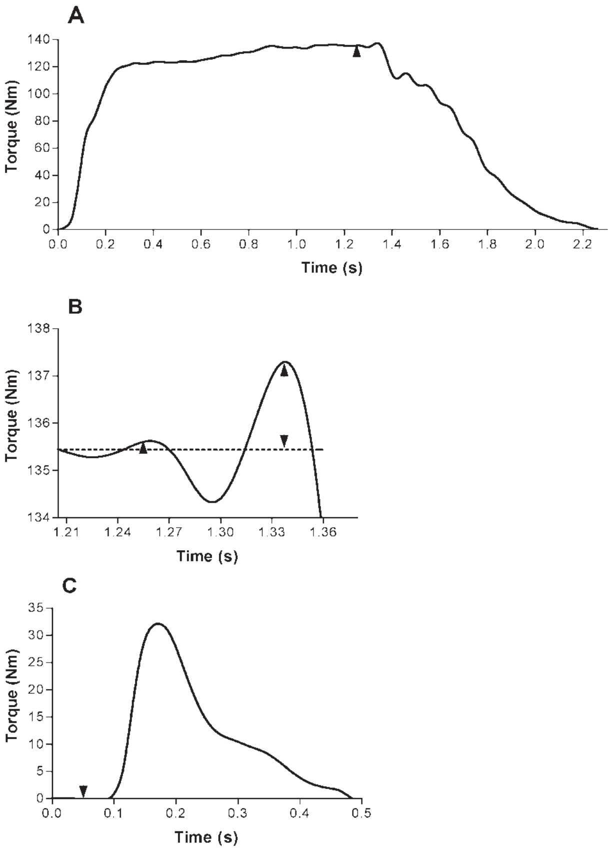

FIGURE 1. Method used to calculate voluntary activation for the isometric condition. **(A)** A torque–time curve from a maximal superimposed voluntary isometric contraction from a representative young subject. The arrow indicates the stimulus trigger. **(B)** Magnified section from **(A)** representing the part of the torque–time curve at which stimulation was delivered. The single-headed arrow indicates the delivery of the stimulus, the dotted line represents the average peak voluntary torque calculated during the 25 ms prior to the stimulus being delivered, and the double-headed arrow indicates interpolated twitch torque amplitude **(C)** A torque–time curve from a potentiated twitch obtained at rest under isometric conditions from the same representative subject in **(A)** and **(B)**. The arrow indicates the stimulus trigger. All data are gravity corrected.

angle peak superimposed torque was attained using a linear regression equation.[2] This procedure was performed using Prism v3.0 for Windows (GraphPad Software, San Diego, California). Interpolated twitch torque was subsequently determined as peak superimposed torque minus voluntary peak torque and was calculated to four decimal places (Figs. 2 and 3).

For all muscle actions, voluntary activation levels were determined by expressing the interpolated twitch torque as a percentage of the peak potentiated evoked twitch torque obtained at rest using the following equation: voluntary activation (%) = [1 − (interpolated twitch torque / peak potentiated evoked twitch torque)] × 100. All trials under the ISO, SHO, and LEN conditions were assessed with the trial yielding the highest voluntary activation level used for subsequent analysis. It should be noted that, due to the small decline (<1%) in peak force necessary to automatically trigger the stimulus during the ISO superimposed contractions, voluntary activation levels under the ISO condition may have been underestimated in both groups. However, this

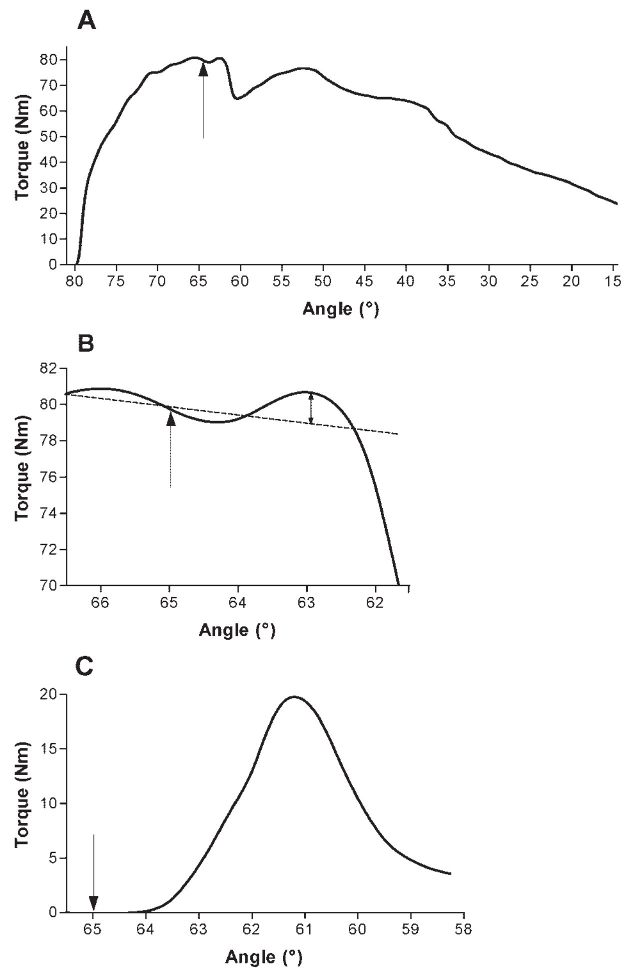

FIGURE 2. Method used to calculate voluntary action for the shortening condition. **(A)** A torque–angle curve from a maximal superimposed shortening contraction from a representative elderly subject. The arrow indicates the stimulus trigger. **(B)** Magnified section from **(A)** representing the part of the torque–angle curve at which the stimulation was delivered. The single-headed arrow indicates the delivery of the stimulus, the dotted line represents the linear extrapolation of the average peak voluntary torque calculated from the 50 ms prior to the stimulus being delivered, and the double-headed arrow indicates interpolated twitch torque amplitude. **(C)** A torque–angle curve from a potentiated twitch obtained at rest under isometric conditions from the same representative subject in **(A)** and **(B)**. The arrow indicates the stimulus trigger. All data are corrected for gravity and viscoelastic forces.

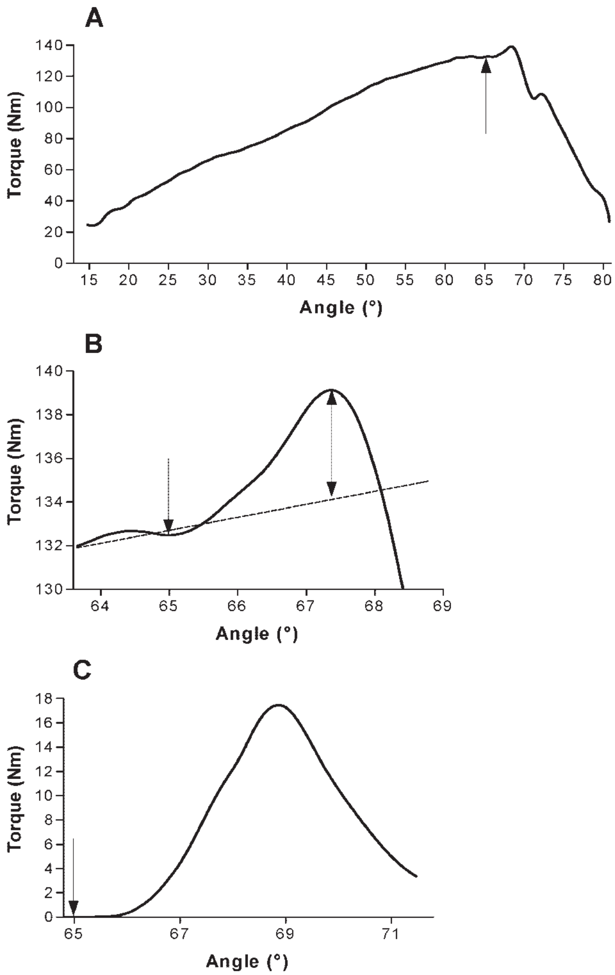

FIGURE 3. Method used to calculate voluntary activation for the lengthening condition. **(A)** A torque–angle curve from a maximal superimposed lengthening contraction from a representative elderly subject. Arrow indicates the stimulus trigger. **(B)** Magnified section from **(A)** representing the part of the torque–angle curve at which stimulation was delivered. The single-headed arrow indicates delivery of the stimulus, the dotted line represents the linear extrapolation of the average peak voluntary torque calculated during the 50 ms prior to the stimulus being delivered, and the double-headed arrow indicates interpolated twitch torque amplitude. **(C)** A torque–angle curve from a potentiated twitch obtained at rest under isometric conditions from the same representative elderly subject in **(A)** and **(B)**. The arrow indicates the stimulus trigger. All data are corrected for gravity and viscoelastic forces.

decline is less than the variance observed in the measurement and is unlikely to have any meaningful impact on the data obtained.

Potentiated Evoked Twitch Contractile Properties. For each muscle action, torque–time curves from the potentiated evoked twitch contractions were averaged across all trials with mean data used to determine the following characteristics: (1) peak potentiated twitch torque (Pt; defined as the highest torque value obtained during the evoked contraction); (2) the rate of torque development (RTD; defined as the mean tangential slope of the twitch torque–time curve between the onset of torque development and Pt); (3) time to peak torque (TPt; defined as the time from evoked torque onset to Pt); (4) the rate of relaxation (RR; defined as the mean tangential slope of the twitch torque–time curve between Pt and $\frac{1}{2}$RT); (5) half-relaxation time ($\frac{1}{2}$RT; defined as the time required for Pt to decline by half); and (6) contraction duration (CD; TPt plus $\frac{1}{2}$RT).[5] Linear regression equations used to calculate mean tangential slope for RTD and RR were calculated using Prism v3.0 for Windows (GraphPad). Torque onset was determined as the point at which torque increased beyond 2 standard deviations above the mean torque value calculated over a 50-ms period immediately prior to stimulation.

Statistical Analysis. All data were log-transformed prior to analysis.[31] Pearson product moment correlations (Pearson's r) were then calculated between muscle actions for each of the measurements of interest. The observed correlation coefficients ($r = 0.56–0.96$; $P < 0.05$) were sufficient to warrant the treatment of the different muscle actions as a single variable due to the high proportion of variance explained by each respective factor. As such, a two-factor mixed factorial analysis of variance (ANOVA) was applied to the entire data set with age group (young vs. elderly) as the between-subjects factor and muscle action (ISO vs. SHO vs. LEN) as the within-subjects factor. Mauchy's test of sphericity and/or Levene's test of equality of error variance did not show statistical significance for any of the analyses ($P \geq 0.18$); thus, sphericity and equal variance across groups were assumed for all tests. If there was a significant main effect and/or interaction, a univariate ANOVA with repeated measures, if necessary, was subsequently used to identify the source of significance. Bonferroni's adjustment for multiple comparisons was applied as appropriate, and level of significance was set at $P < 0.05$. All statistical procedures were performed using SPSS v14.0 for Windows (SPSS, Inc., Chicago, Illinois). Magnitudes of the age-associated differences were quantified as: $\Delta(\%) = [(\text{young} - \text{elderly}) / \text{young}] \times 100$. Data are presented as mean ± standard deviation.

RESULTS

Voluntary Peak Torque. For the young subjects, voluntary peak torque attained during the superimposed contractions under the ISO, SHO, and LEN

Table 1. Potentiated evoked twitch properties for the isometric, shortening, and lengthening conditions in the young and elderly subjects.

Group	Muscle action	Pt(N·m)	Pt/PT Ratio	RTD (N·m s^{-1})	RR (N·m s^{-1})	TPt(ms)	1/2RT(ms)	CD(ms)
Young(n = 18)	ISO	32.7 ± 13.4	0.25 ± 0.06	455 ± 195†	305 ± 141	91.0 ± 6.6¶	59.4 ± 11.5‡	150.4 ± 14.8¶
	SHO	25.8 ± 10.0*	0.24 ± 0.08	239 ± 97†	260 ± 123*	123.9 ± 21.9	56.8 ± 9.2	180.7 ± 23.2
	LEN	30.6 ± 10.6	0.26 ± 0.07	319 ± 144†	327 ± 147	116.5 ± 22.9	52.6 ± 9.4	169.1 ± 25.1
Elderly(n = 12)	ISO	22.4 ± 5.1§	0.26 ± 0.07	286 ± 76†§	194 ± 88§	98.1 ± 9.8§¶	67.5 ± 17.2‡	165.6 ± 21.1§¶
	SHO	16.6 ± 6.3*§	0.24 ± 0.07	128 ± 30†§	156 ± 98‡§	146.0 ± 20.4§	67.8 ± 21.4	213.8 ± 29.4§
	LEN	21.8 ± 7.0§	0.22 ± 0.07	178 ± 71†§	211 ± 106§	142.4 ± 23.8§	59.8 ± 13.5	202.2 ± 22.4§

ISO, isometric contraction; SHO, shortening contraction; LEN, lengthening contraction; Pt, peak potentiated twitch torque; PT, voluntary peak torque; RTD, rate of torque development; RR, rate of relaxation; TPt, time to Pt; 1/2RT, half-relaxation time; CD, contraction duration. Values presented as mean ± standard deviation.

[*]Significant difference from the ISO and LEN actions in the respective group (P < 0.05).

[†]Significant differences between all muscle actions in the respective group (P < 0.05).

[‡]Significant differences from the LEN condition in the respective group (P < 0.05).

[§]Significant difference from the young subjects (P < 0 .05).

[#]Significant difference from the SHO and LEN actions in the respective group (P < 0.05).

conditions were 130 ± 49 N · m, 109 ± 38 N · m, and 123 ± 48 N · m, respectively. Within-group analyses revealed that voluntary peak torque in the young was significantly lower during the SHO action compared with both the ISO and LEN conditions (P <0.05). For the elderly subjects, voluntary peak torque attained during the superimposed contractions under the ISO, SHO, and LEN actions were 89 ± 24 N · m, 72 ± 21 N · m, and 103 ± 28 N · m, respectively. Within-group analyses revealed that voluntary peak torque in the elderly was significantly lower during the SHO action compared with both the ISO and LEN conditions ($P < 0.01$), and lower during the ISO actions compared with the LEN condition ($P < 0.05$). Between-group analyses revealed voluntary peak torque was significantly lower for the elderly during the ISO and SHO actions (−31% and −28%, respectively) ($P < 0.01$). In contrast, the lower LEN voluntary peak torque in the elderly, compared with the young (−17%), did not reach statistical significance ($P = 0.18$).

Voluntary Activation. For the young subjects, voluntary activation levels for the ISO, SHO, and LEN actions were 97.7 ± 2.3%, 98.2 ± 2.1%, and 96.8 ± 4.8%, respectively. For the elderly subjects, voluntary activation levels for the ISO, SHO, and LEN actions were 98.2 ± 1.5%, 98.9 ± 1.8%, and 98.5 ± 2.6%, respectively. No significant differences were observed for level of voluntary activation within subjects or between age groups for any of the muscle actions assessed (P >0.05).

Potentiated Evoked Twitch Properties. Potentiated evoked twitch properties for the ISO, SHO, and LEN conditions for the young and elderly are presented in Table 1. Pt was significantly lower for the SHO condition, compared with the ISO and LEN conditions, in both age groups ($P < 0.01$). Pt was significantly lower for the elderly across all conditions ($P < 0.05$). Pt/voluntary peak torque ratio (Pt/PT) was not significantly different within or between subjects ($P > 0.05$). In the young, RTD was significantly higher for the ISO condition compared with the LEN condition ($P < 0.01$) and significantly higher for the LEN condition compared with the SHO condition ($P < 0.05$). In the elderly, RTD was also significantly higher for the ISO condition compared with the LEN condition ($P < 0.01$) and significantly higher for the LEN condition compared with the SHO condition ($P < 0.01$). RTD was significantly lower for the elderly compared with the young across all conditions ($P < 0.01$).

RR was significantly lower for the SHO condition compared with both the ISO ($P < 0.05$) and LEN conditions in the young ($P < 0.01$), whereas RR was significantly lower for the SHO condition compared with the LEN condition in the elderly ($P < 0.05$). RR was significantly lower for the elderly compared with the young across all muscle actions ($P < 0.05$). TPt was significantly shorter for the ISO condition compared with the SHO and LEN conditions in both age groups ($P < 0.01$), and it was significantly longer for the elderly compared with the young across all muscle actions, demonstrating increases of 8%, 17%, and 22% for the ISO, SHO, and LEN conditions, respectively ($P < 0.05$). $\frac{1}{2}$RT was significantly shorter for the LEN condition compared with the ISO condition in both age groups ($P < 0.05$), and a trend was observed for $\frac{1}{2}$RT to be significantly longer during the SHO condition for the elderly compared with the young ($P = 0.06$). CD was significantly shorter for the ISO action compared with the SHO and LEN conditions in both age groups ($P < 0.01$), and it was significantly longer for the elderly compared with the young across all muscle actions ($P < 0.05$).

DISCUSSION

The results of this study provide further support for the relative maintenance of LEN voluntary peak torque with age as compared with ISO and SHO efforts. Moreover, we failed to observe an age-associated change in voluntary activation levels during the static or dynamic maximal voluntary contractions. In contrast, some potentiated twitch properties were influenced by age; however, the magnitude and direction of the changes observed were similar among muscle actions. Based on these results, it appears that the neuromuscular mechanisms contributing to the attenuated reduction in LEN voluntary peak torque with age probably do not involve contraction-specific changes in either neural drive or peripheral contractile function.

We observed age-associated reductions of 31% and 28% for ISO and SHO voluntary peak torque, respectively, which are similar to previous studies that reported age-associated reductions in peak ISO and SHO muscle strength of 20–35% when performed at 0–120°/s (0–2.09 rad/s).[5,32] Furthermore, the 17% reduction we observed in LEN voluntary peak torque in the elderly is also in agreement with previous studies, where less marked reductions of ∽10–25% were reported at similar contraction velocities.[5,23,24] Age-related reductions in peak muscle strength under ISO and slow to moderate velocity SHO conditions can be largely explained by aging atrophy. Relative losses in ISO and SHO peak strength and muscle mass with age are highly comparable,[12,15] and data examining age-related changes in normalized strength (i.e., strength per unit of muscle mass) during ISO and SHO actions are also comparable.[5,23,24]

In contrast to those findings, age-related changes in peak muscle strength under LEN conditions appear to be relatively independent of aging atrophy, as relative strength losses appear to be less than the relative decreases observed in muscle mass.[5,23,24] As such, it appears that neuromuscular mechanisms are likely to be involved in the relative preservation of LEN muscle strength with age. One possible mechanism not examined herein involves age-related changes in antagonist coactivation. A previous study reported that increased coactivation does not account for the age-related decreases in ISO and SHO peak torque or the attenuated reduction in LEN peak torque of the ankle dorsiflexors.[17] Furthermore, the comparable Pf/PT ratios we observed in this study within and between groups provides some evidence that age-related adjustments in antagonist coactivation were not substantial in the elderly.

Previous studies of age-associated changes in voluntary activation have primarily involved ISO muscle actions and provided equivocal results.[10,16,33,34] Stevens et al.[34] proposed that such discrepancies between studies may be related to differences in the stimulation parameters used. Most studies, but not all,[6] that demonstrated an age-associated reduction in voluntary activation levels[16,34] used a high-frequency train of pulses during contraction. The studies that did not detect an age-associated change[33] often, but not always,[9] used single-pulse stimulation. A high-frequency train of pulses may increase measurement sensitivity, as higher muscle forces can be elicited. They may be better for detecting a change in interpolated twitch amplitude.[16,34] However, high-frequency stimulation can cause considerable discomfort to subjects when assessing a large muscle group such as the knee extensors. Furthermore, the risk of injury associated with high-frequency stimulation during forced muscle lengthening must also be considered (e.g., musculotendinous or joint injury due to excessive strain). Although it is intuitive that a high-frequency doublet (paired stimuli) would be an acceptable compromise between a single pulse and a high-frequency train of pulses, no significant difference in the superimposed force to peak voluntary force ratio was apparent when a single twitch, doublet, or quintuplet were compared.[4] In addition, both lack of a familiarization session and an inadequate number of trials have been reported to increase the variability of voluntary activation data in the elderly.[13] This may also assist in explaining inconsistencies between studies.

Very few studies have examined age-associated changes in voluntary activation during dynamic actions. White and Harridge[35] compared maximal voluntary and electrically induced peak forces of the ankle plantarflexors in the young and elderly during SHO actions and reported that voluntary activation levels were comparable between groups at velocities up to 240°/s. More recently, Klass et al.[17] used the central activation ratio to examine the ankle dorsiflexors in the young and elderly and reported that voluntary activation levels were maximal or near maximal under ISO, SHO, and LEN conditions in both age groups at velocities up to 100°/s (1.75 rad/s). Despite the fact that we employed the twitch interpolation technique and performed our assessments on a muscle group that is usually more difficult to activate than the ankle dorsiflexors, our results are highly comparable with those of Klass et al.[17] and demonstrate voluntary activation levels of >95% during all muscle actions in both age groups.

Studies comparing evoked twitch responses between static and dynamic muscle actions are scarce. Gravel et al.[9] compared resting twitch properties of the ankle plantarflexors under static and slow dynamic conditions in young adults and reported a lower Pt during the SHO condition when compared with the ISO and LEN conditions, whereas Pt was similar between the ISO and LEN conditions. However, no significant differences in twitch time course (i.e., TPt or $\frac{1}{2}$RT) were reported between conditions.[9] Our findings regarding Pt are similar to those of Gravel et al.[9]; however, we also observed significant differences between conditions in temporal twitch characteristics (see Table 1). Furthermore, our data show that the magnitude and direction of the differences in the twitch characteristics observed between conditions were similar among age groups. Such results suggest that aging was not associated with contraction-specific adjustments in peripheral contractile function.

We postulated that the twitch response during the LEN condition would yield greater Pt and faster contractile times. Our inability to detect such a phenomenon may have been due to the use of single-pulse stimulation. Joyce et al.[14] studied the static and dynamic contractile properties of cat soleus muscle and reported that low-frequency and high-tetanic stimulation produced the highest Pt during the ISO and LEN conditions, respectively, whereas SHO Pt was typically lowest for all muscle actions regardless of the type of stimulation applied. Accordingly, Joyce et al.[14] speculated that, when a train of pulses is delivered at a frequency of <20 Hz, actomyosin cross-bridges cannot be easily maintained concurrent with muscle lengthening or shortening. Furthermore, our results were likely influenced by the relatively slow velocity of stretch applied to the passive muscle,[1] which probably impaired the contribution of passive elements to Pt production.

Our findings extend those from previous studies demonstrating altered resting[5,33] and potentiated[21] twitch contractile properties with age under ISO conditions. In addition, this is the first study to report such changes under SHO and LEN conditions. The reductions in Pt and slowing in the rate of contraction observed are thought to be related to age-associated changes in muscle morphology characterized by the selective loss of type II fibers and the preferential atrophy of those type II fibers remaining.[22] Furthermore, intrinsic muscle function is also impaired with age, as the maximal unloaded shortening velocity of type I and/or type II muscle fibers is reduced[19] due to a decline in the rate of excitation–contraction coupling[27] and the speed of cross-bridge cycling.[11] In addition to altered fiber function, the age-related alterations in evoked twitch properties are also likely to be influenced by the cumulative effects of age-related adaptations in tendon elasticity and muscle architecture; increased tendon compliance in the elderly may dampen force development,[26] whereas decreased muscle fiber pennation angle may enhance the rate of contraction/relaxation.[20]

In this investigation we have attempted to induce postactivation potentiation of the twitch responses by having subjects perform a maximal voluntary contraction of the same muscle action and velocity immediately prior to each twitch assessment. Our aim was to elicit a contractile response most likely to represent the functional characteristics of active muscle. The postactivation potentiation effect is thought to be related to the phosphorylation of myosin regulatory light chains during the conditioning contraction, which increases the sensitivity of the contractile apparatus to activation by Ca^{2+},[18] and enhances the ability of the cross-bridges to enter a forcing–producing state.[28] Although an earlier study concluded that the level of postactivation potentiation in human muscle is not related to the type of maximal conditioning contraction,[3] more recent work has suggested that postactivation potentiation induced through a maximal ISO conditioning contraction may be greatest during SHO muscle actions compared with LEN efforts.[2] However, despite these discrepancies, interpretation of the results obtained remains valid, as the experimental conditions were identical between age groups.

In conclusion, the results of this study provide additional support for the relative maintenance of LEN muscle strength with age. Moreover, these data extend the results from previous studies by demonstrating that the neuromuscular mechanisms that contribute to this phenomenon do not involve contraction-specific changes in either voluntary activation or peripheral contractile function. Although contraction-specific changes in potentiated twitch properties with age were not observed, it is possible that the attenuated loss of LEN muscle strength with age is related to the slowing of muscle contraction,[29,30] where the functional consequence of contractile slowing for LEN voluntary peak torque may not be apparent at relative low torque levels. High levels of LEN voluntary peak torque may be necessary in order to absorb the elasticity from the musculotendinous unit prior to such a mechanism contributing to torque production.

The authors thank Associate Professor David McKinnon and Dr. Eric Drinkwater for providing expert statistical advice and assistance with data analysis.

REFERENCES

1. Babault N, Maffiuletti NA, Pousson M. Postactivation potentiation in human knee extensors during dynamic passive movements. Med Sci Sports Exerc 2008;40:735–743.
2. Babault N, Pousson M, Ballay Y, van Hoecke J. Activation of human quadriceps femoris during isometric, concentric and eccentric contractions. J Appl Physiol 2001;91:2628–2634.
3. Baudry S, Duchateau J. Postactivation potentiation in human muscle is not related to the type of maximal conditioning contraction. Muscle Nerve 2004;30:328–336.
4. Behm DG, St-Peirre DMM, Perez D. Muscle inactivation: assessment of interpolated twitch technique. J Appl Physiol 1996;81:2267–2273.
5. Cannon J, Kay D, Tarpenning KM, Marino FE. Normalized lengthening peak torque is associated with temporal twitch characteristics in elderly women but not young women. Acta Physiol 2006;188:53–62.
6. De Serres SJ, Enoka RM. Older adults can maximally activate the biceps brachii muscle by voluntary command. J Appl Physiol 1998;84:284–291.
7. Earles D, Vardaxis V, Koceja D. Regulation of motor output between young and elderly subjects. Clin Neurophysiol 2001; 112:1273–1279.
8. Enoka RM. Eccentric contractions require unique activation strategies by the nervous system. J Appl Physiol 1996;81:2339–2346.
9. Gravel D, Bélanger A, Richards C. Study of human muscle contraction using electrically evoked twitch responses during passive shortening and lengthening movements. Eur J Appl Physiol 1987;56:623–627.
10. Harridge SDR, Kryger A, Stensgaard A. Knee extensor strength, activation and size in very elderly people following strength training. Muscle Nerve 1999;22:831–839.
11. Höök P, Sriramoju V, Larsson L. Effects of aging on actin sliding speed on myosin from single skeletal muscle cells of mice, rats, and humans. Am J Physiol Cell Physiol 2001;280: C782–C788.
12. Ivey FM, Tracy BL, Lemmer JT, Ness Aviver M, Metter EJ, Fozard JL, et al. Effects of strength training and detraining on muscle quality: age and gender comparisons. J Gerontol Series A Biol Sci Med Sci 2000;55A:B152–B157.
13. Jakobi JM, Rice CL. Voluntary muscle activation varies with age and muscle group. J Appl Physiol 2002;93:457–462.
14. Joyce GC, Rack PMH, Westbury DR. The mechanical properties of cat soleus muscle during controlled lengthening and shortening movements. J Physiol 1969;204:461–474.
15. Jubrias SA, Odderson IR, Esselman PC, Conely KE. Decline in isokinetic force with age: muscle cross-sectional area and specific force. Pflügers Arch Eur J Appl Physiol 1997;434:246–253.
16. Kent-Braun JA, Le Blanc R. Quantification of central activation failure during maximal voluntary contractions in humans. Muscle Nerve 1996;19:861–869.
17. Klass M, Baudry S, Duchateau J. Aging does not affect voluntary activation of the ankle dorsiflexors during isometric, concentric, and eccentric contractions. J Appl Physiol 2005; 99:31–38.
18. Klug GA, Botterman BR, Stull JT. The effect of low frequency stimulation on myosin light chain phosphorylation in skeletal muscle. J Biol Chem 1982;257:4688–4690.
19. Krivickas KL, Luh D, Wilkins J, Hughes VA, Roubenoff R, Frontera WR. Age- and gender-related differences in maximum shortening velocity of skeletal muscle fibers. Am J Phys Med Rehabil 2001;80:447–455.
20. Kubo K, Kanehisa H, Azuma K, Ishizu M, Kuno SY, Okada M, et al. Muscle architechural characteristics in young and elderly women. Int J Sports Med 2003;24:125–130.
21. Kuu S, Gapeyeva H, Ereline J, Paasuke M. Twitch contractile properties of plantarflexor muscles in young and middle-aged recreationally physically active and non-active women. Aging Clin Exp Res 2007;19:48–54.
22. Larsson L, Karlsson J. Isometric and dynamic endurance as a function of age and skeletal muscle characteristics. Acta Physiol Scand 1978;104:129–136.
23. Lindle RS, Metter EJ, Lynch NA, Fleg JL, Fozard JL, Tobin J, et al. Age and gender comparisons of muscle strength in 654 women and men aged 20–93 yr. J Appl Physiol 1997;83:1581–1587.
24. Lynch NA, Metter EJLRS, Fozard JL, Tobin JD, Roy TA, Fleg JL, et al. Muscle quality. I. Age-associated differences between arm and leg muscle groups. J Appl Physiol 1999;86:188–194.
25. Murray MP, Duthie EH, Gambert SR, Sepic SB, Mollinger LA. Age-related differences in knee muscle strength in walking women. J Gerontol 1985;40:275–280.
26. Narici MV, Maganaris CN. Plasticity of the muscle–tendon complex with disuse and aging. Exerc Sport Sci Rev 2007;35: 126–134.
27. Payne AM, Delbono O. Neurogenesis of excitation–contraction uncoupling in aging skeletal muscle. Exerc Sports Sci Rev 2004;32:36–40.
28. Persechini A, Stull JT, Cooke R. The effect of myosin phosphorylation on the contractile properties of skinned rabbit skeletal muscle fibers. J Biol Chem 1985;260:7951–7954.
29. Porter MM, Myint A, Kramer JF, Vandervoort AA. Concentric and eccentric knee extension strength in older and younger men and women. Can J Appl Physiol 1995;20:429–439.
30. Porter MM, Vandervoort AA. Standing strength training of the ankle plantar and dorsiflexors in older women, using concentric and eccentric contractions. Eur J Appl Physiol 1997;76:62–68.
31. Portney LG, Watkins MP. Foundations of clinical research: applications to practice. Upper Saddle River, NJ: Prentice Hall; 2000.
32. Roos MR, Rice CL, Vandervoort AA. Age-related changes in motor unit function. Muscle Nerve 1997;20:679–690.
33. Roos MR, Rice CL, Connelly DM, Vandervoort AA. Quadriceps muscle strength, contractile properties, and firing rates in young and old men. Muscle Nerve 1999;22:1094–1103.
34. Stevens JE, Stackhouse SK, Binder-MacLeod SA, Snyder-Mackler L. Are voluntary muscle activation deficits in older adults meaningful? Muscle Nerve 2003;27:99–101.
35. White M, Harridge S. At high angular velocities voluntary activation limits maximal isokinetic torque generation in elderly and young human triceps surae [abstract]. J Physiol 1990;429:52P.