Experimental Gerontology 52 (2014) 70–76

Contents lists available at ScienceDirect

Experimental Gerontology

journal homepage: www.elsevier.com/locate/expgero

The effect of knee joint angle on plantar flexor power in young and old men

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ARTICLE INFO

Article history:
Received 7 October 2013
Received in revised form 19 December 2013
Accepted 9 January 2014
Available online 23 January 2014

Section Editor: Christiaan Leeuwenburgh

Keywords:
Aging
Force–velocity
Muscle
Strength
Triceps surae

ABSTRACT

Human adult aging is associated with a loss of strength, contractile velocity and hence, power. The principal plantar flexors, consisting of the bi-articular gastrocnemeii and the mono-articular soleus, appear to be affected differently by the aging process. However, the age-related effect of knee joint angle on the torque–angular velocity relationship and power production of this functionally important muscle group is unknown. The purpose was to determine whether flexing the knee, thereby reducing the gastrocnemius contribution to plantar flexion, would exacerbate the age-related decrements in plantar flexion power, or shift the torque–angular velocity relationship differently in older compared with young men. Neuromuscular properties were recorded from 10 young (~25 y) and 10 old (~78 y) men with the knee extended (170°) and flexed (90°), in a randomized order. Participants performed maximal voluntary isometric contractions (MVCs), followed by maximal velocity-dependent shortening contractions at pre-set loads, ranging from 15 to 75% MVC. The young men were ~20–25% stronger, ~12% faster and ~30% more powerful than the old for both knee angles ($P < 0.05$). In both age groups, isometric MVC torque was ~17% greater in the extended than flexed knee position, with no differences in voluntary activation (>95%). The young men produced 7–12% faster angular velocities in the extended knee position for loads ≤30% MVC, but no differences at higher loads; whereas there were no detectable differences in angular velocity between knee positions in the old across all relative loads. For both knee angles, young men produced peak power at 43.3 ± 9.0% MVC, whereas the old men produced peak power at 54.8 ± 7.9% MVC. These data indicate that the young, who have faster contracting muscles compared with the old, can rely more on velocity than torque for generating maximal power.

1. Introduction

Muscle power, the product of angular velocity and torque generation, is a key measure in quantifying physical impairments in older adults (Bean et al., 2010; Pojednic et al., 2012). Maximal power is achieved through an optimal interplay between angular velocity of shortening and torque production whereby both factors are operating at respective submaximal levels. Therefore, because skeletal muscle is most efficient when operating at submaximal velocities and torque (Lieber and Ward, 2011), power likely represents a better proxy of the functional capacity of muscle than measures of angular velocity or torque alone. Indeed the age-related loss of torque combined with slower contractile velocities produce a greater relative loss of power than the percentage loss in either factor separately (Power et al., 2013). However, impairments in contractile speed may be the more impactful factor accounting for decrements in maximal power production in older individuals (Dalton et al., 2010, 2012; Pojednic et al., 2012). To compensate for their slower contracting muscles, older adults likely rely more on torque to generate peak power than do young adults. Whether and how these age-related changes affect power production has not been explored comprehensively, and the unique features of the triceps surae muscle group may provide a useful model to provide further understanding.

As the dominant plantar flexor (Cresswell et al., 1995; Fukunaga et al., 1992), the triceps surae share an important role in locomotion, standing balance and many activities of daily living. For example, ankle plantar flexion power is a critical factor in modulating walking speed (Liu et al., 2008). However, the individual components of this functionally complementary muscle group display different anatomical, electrophysiological, histochemical, and mechanical characteristics (Tucker et al., 2005). For example, the soleus is a habitually active postural muscle that is comprised of fewer than 15% fast twitch motor

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0531-5565/$ – see front matter © 2014 Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.exger.2014.01.011

units equating to less than 20% fast twitch muscle fiber area; whereas the gastrocnemeii are less active during quiet stance and are composed of ~50% fast twitch motor units and ~50% muscle fiber area (Costill et al., 1976; Johnson et al., 1973; Joseph and Nightingale, 1952; Trappe et al., 2001). The bi-articular nature of the gastrocnemeii complicates control of plantar flexion function. For example, manipulating ankle angle alters the fascicle length of all three heads of the triceps surae to a similar extent (Kawakami et al., 1998). However, a change in knee angle affects the fascicle length of the gastrocnemeii only (Kawakami et al., 1998) which in turn alters the torque–length relationship and thereby impacts the whole musclulotendinous unit (Arampatzis et al., 2006). Hence, knee flexion leads to reductions in isometric (Cresswell et al., 1995) and isokinetic (Wakahara et al., 2007) torque generation and velocity-dependent power production (Dalton et al., 2013) of the plantar flexors in young adults. Yet, how these factors may affect triceps surae function in the aged system remains unclear.

With adult aging neuromechanical function of the triceps surae is complicated by disparate neuromuscular changes of the two main muscles. For example, motor unit number estimates (Dalton et al., 2008), maximal motor unit discharge rates (Dalton et al., 2009) and muscle architecture (Fujiwara et al., 2010; Morse et al., 2005) of the soleus are largely maintained with adult aging relative to other limb muscles at least until the 8th decade; whereas the gastrocnemeii are more susceptible to sarcopenic changes (Fujiwara et al., 2010; Morse et al., 2005). The greater alterations of the gastrocnemeii will shift the plantar flexor torque–angular velocity relationship down and to the left with the knee extended, which may cause older adults to rely more upon the soleus for plantar flexion power than the young. However, it is unclear whether disadvantaging one muscle in a synergistic muscle group – that is already more compromised with aging – will exacerbate the age-related shift of the torque–angular velocity relationship and impair plantar flexor power production capacity even further compared with young.

The purpose was to investigate the effect of aging on the torque–angular velocity relationship of a synergistic muscle group involved in plantar flexion. More specifically, we utilized two dynamic testing modalities, torque-dependent (isokinetic) and velocity-dependent (isotonic) contractions to elucidate the role of the bi-articular gastrocnemeii in both an optimal (extended knee) and disadvantaged (flexed knee) torque–length relationship on maximal plantar flexion power generation in healthy older adults. We expected that the older adults would rely more on torque to produce peak power due to their slower contracting muscles than the young. In the flexed knee position, we hypothesized that both age groups would exhibit reduced power. However, because the gastrocnemeii exhibit greater age-related alterations than the soleus, we expected that flexing the knee, which typically disadvantages the gastrocnemeii, would exhibit less of a decrease in angular velocity and hence power production capacity in the older men than young.

2. Materials and methods

2.1. Participants

Ten recreationally active young men (age: 26.3 ± 3.4 y, height: 178.1 ± 6.1 cm, body mass: 80.1 ± 3.4 kg) were recruited from the local university population, and ten healthy older men (age: 77.6 ± 4.4 y, height: 175.7 ± 3.8 cm, body mass: 83.7 ± 11.3 kg) participated in this study. The older participants were living independently in the community, free of neuromuscular and orthopedic injuries/disorders, healthy and recreationally active. All older adults were recruited from a senior's activity program at the university. This program is designed to maintain cardiovascular fitness, muscular endurance and flexibility using light to moderate exercise. The local university's ethics review board for experimentation on humans granted approval for the study. All participants provided oral and written informed consent prior to experimental testing.

2.2. Experimental arrangement

Plantar flexion torque, velocity and ankle position in the isometric, isokinetic and isotonic modes were recorded using a Biodex System 3 multi-joint dynamometer (Biodex Medical Systems Inc., Shirley, NY, USA). All tests were performed on the dominant (right) leg. Participants performed plantar flexion actions in two positions: with the knee extended to 170° (with full extension being 180°) and the knee flexed to 90°. Participants were seated comfortably in a reclined position with the hip joint at 90° and the ankle at a neutral angle ($0° = $ neutral) for isometric contractions and for the starting point of all dynamic contractions. Range of motion for the dynamic contractions was set from neutral to 30° of plantar flexion. The foot was secured to the footplate using a heel binding with an adjustable strap across the dorsum of the foot near the ankle joint. Two Velcro straps were also secured distally over the foot and across the toes. During all contractions, the participants were secured to the Biodex chair with inelastic straps around the shoulders and waist. A thigh support with an inelastic strap was used to stabilize the lower limb and minimize involvement of the thigh muscles. The ankle joint was aligned with the axis of rotation of the dynamometer. Plantar flexion torques, velocities and positions were sampled at 100 Hz using a 12-bit analog-to-digital converter (Power 1401; Cambridge Electronic Design, Cambridge, UK) and digitized online using Spike2 software (Cambridge Electronic Design).

Single twitches were evoked electrically from the plantar flexors using 100-μs square wave pulse set at a maximal voltage of 400 V (Digitimer stimulator, model DS7AH; Digitimer Ltd., Welwyn Garden City, UK). A commercially available clinical stimulating bar electrode (Chalgren Enterprises Inc., Gilroy, California, United States) was held firmly in the distal portion of the popliteal fossa between the origins of the heads of the gastrocnemeii to electrically activate the tibial nerve.

2.3. Experimental procedures

Data were collected during a single visit to the neuromuscular laboratory, in which participants from both groups performed isometric and dynamic shortening contractions at two different knee angles. The order of knee angle testing was assigned pseudo-randomly to counteract any effects of fatigue, but the procedures were performed in an identical sequence at each knee angle. Between testing sessions for each knee angle, participants rested for at least 20 min to eliminate any effects of fatigue.

Once participants were positioned in the Biodex, plantar flexor twitch torque was evoked by increasing the current gradually (~20–30 mA) until twitch torque peaked with no further enhancement in amplitude from increasing current. To ensure full activation of all motor axons, the current was then increased a further 20% (range: 240–850 mA at 400 V). Following the electrically evoked contractions, participants attempted three ~5-s maximal isometric voluntary contractions (MVCs). An additional MVC was performed if the first three varied in peak torque amplitude by more than 5%. Each MVC attempt included a supramaximal twitch delivered ~1-s prior (at rest), another during peak MVC torque (T_s) and another ~1-s following (T_r) when the plantar flexors were relaxed fully. Twitch torque amplitudes during and post-plantar flexion MVC were used to assess voluntary activation via the interpolated twitch technique [$\% \text{ activation} = [1 - (T_s / T_r)] \times 100$]. Participants received verbal encouragement during all maximal voluntary efforts and visual feedback of torque output on a computer monitor. All isometric MVCs were separated by at least 3 min of rest.

Three minutes following the isometric MVC attempts, participants were familiarized with the maximal effort isokinetic ($30° \cdot s^{-1}$) shortening contractions by performing three consecutive attempts separated by ~1 s. During these contractions, participants were asked to plantar flex maximally against the foot plate as it moved at a fixed isovelocity of $30° \cdot s^{-1}$ through 30° of ankle joint excursion. Upon completion of each isokinetic contraction, the dynamometer was returned (~1 s) to the starting position by the investigator while the subject relaxed his leg muscles. Following 3 min of rest, participants performed two baseline isokinetic attempts. Participants were encouraged verbally and given visual feedback of the torque signal to ensure a maximal effort. These contractions were performed to determine the optimal angle of plantar flexion torque production.

Following another 3 min of rest, the dynamometer was switched to the isotonic mode whereby the task was dependent upon the ability of the participant to voluntarily move a fixed resistance as fast as possible (i.e., unconstrained velocity) through the 30° range of motion. During all dynamic efforts, participants were instructed to move the dynamometer "as fast and as hard as possible" and were provided verbal encouragement. This measure has been found to be reliable and reproducible (Power et al., 2011). All participants were provided visual feedback of the velocity profile on a computer monitor. Once a shortening contraction was complete the participant relaxed and, the dynamometer returned the foot passively to the original starting position at a speed of ~30°·s^{-1}. Familiarization involved ~5 dynamic contractions separated by short rest intervals of ~5–10 s with a pre-set resistance of 20% MVC. This portion of the session was followed by 3 min of rest. Then, the participants performed pairs of unconstrained velocity shortening contractions at 6 different loads that were normalized to the isometric MVC for each respective knee angle (15, 20, 30, 45, 60, and 75% MVC). The pairs of velocity-dependent contractions were separated by ~30 s of rest. Participants were blinded to the resistance they were being asked to move and the order of these resistances was randomized to minimize potential effects of fatigue.

2.4. Data analysis and statistics

Electrically evoked isometric contractile function of the plantar flexors was assessed by peak twitch torque (N·m), time to peak twitch torque (ms) and half relaxation time (ms) of the twitch, which were taken from the twitch evoked ~1 s prior to the MVC attempt. All voluntary and evoked isometric values were taken from the MVC with the maximum torque amplitude and the corresponding twitch responses. Dynamic torque and power were taken from the maximum torque value for the isokinetic actions. Angular velocity and power of the velocity-dependent (isotonic) task were taken from the contraction with the maximum angular velocity. Power (W) was calculated as the product of the peak torque generated by the participant (N·m) and the angular velocity (rad·s^{-1}) of the dynamometer during the isokinetic task. For the velocity-dependent movements, power (W) was calculated as the product of angular velocity (rad·s^{-1}) and the generated torque (N·m) which achieved maximal power. To assess the effect of knee angle, the position of ankle plantar flexion where instantaneous peak torque or peak velocity occurred, was analyzed from the isokinetic and velocity-dependent contractions, respectively.

Data were analyzed using SPSS version 17 (SPSS, Chicago, IL). A 2-way ANOVA (knee angle × age) with repeated measures was used to determine differences for all isometric and isokinetic data. A 3-way ANOVA (knee angle × age × load) with repeated measures was used to analyze all data from the unconstrained velocity contractions. Subsequently, when a significant main effect or interaction was observed, a Tukey post hoc analysis was performed to test where significant differences occurred. The alpha level was set at $P \leq 0.05$. Descriptive statistics are reported as means ± standard deviations (SDs) in tables and means ± standard error of measurement (SEMs) in figures.

3. Results

3.1. Torque-dependent measures

A descriptive summary of the neuromuscular properties of the plantar flexors in young and old men is provided in Table 1. Young men were ~25% and ~20% stronger than old men in both the extended and flexed knee positions for isometric and isokinetic MVC torque, respectively ($P < 0.05$), despite no detectable differences in voluntary activation (Table 1). Both age groups were ~17% and ~19% stronger equally in the extended versus the flexed knee position for the isometric and isokinetic MVC, respectively ($P < 0.05$; Table 1). The electrically evoked twitch was faster ($P < 0.05$) and exhibited a trend for a higher torque amplitude ($P = 0.08$) in the young than old men for both knee angles (Table 1). With the knee extended, peak twitch amplitude was greater ($P < 0.05$) and the time to peak twitch torque was shorter than the flexed knee (Table 1) for both groups. Because peak twitch torque amplitudes varied for knee angle and age, evoked contractile speeds were normalized to the respective twitch amplitudes. Normalized time to peak twitch torque and half relaxation time were faster in the extended than flexed knee ($P < 0.05$) with faster speeds for both parameters in the young than old men ($P < 0.05$; Table 1). For the slow isokinetic task, extending the knee shifted the optimal position of torque production in the young to a greater plantar flexion angle (i.e., shorter muscle lengths) compared with the flexed position. However, there were no detectable differences in optimal angle of torque production for the older adults when knee angle was changed (Table 1). Therefore, the older men reached optimal torque production at presumed shorter muscle lengths (flexed knee) than the young ($P < 0.05$).

Table 1
Neuromuscular properties of the plantar flexors.

	Young (n = 10)			Old (n = 10)		
	Extended	Flexed	% difference	Extended	Flexed	% difference
MVC (N·m)	192.3 ± 37.1	158.9 ± 25.1[a]	**17**	154.2 ± 18.6[b]	128.8 ± 28.1[a,b]	**17**
Voluntary activation (%)	96.3 ± 1.4	96.4 ± 2.7	–	95.0 ± 2.8	95.6 ± 2.6	1
IsokMVC (N·m)	127.3 ± 21.9	103.7 ± 19.9[a]	**19**	101.4 ± 13.7[b]	81.2 ± 16.6[a,b]	**20**
Optimal angle (°)	9.4 ± 1.8	8.0 ± 1.7[a]	**15**	10.6 ± 1.5	10.9 ± 2.1[b]	3
Peak twitch torque (N · m)	28.9 ± 7.5	21.1 ± 6.5[a]	**27**	22.3 ± 4.6[c]	17.7 ± 4.7[a,c]	**21**
TPT (ms)	120.4 ± 21.1	129.5 ± 15.6[a]	**8**	133.9 ± 16.1[c]	153.9 ± 25.6[a,b]	**15**
HRT (ms)	88.7 ± 14.3	93.4 ± 10.2	5	108.5 ± 10.6[b]	105.6 ± 9.6[b]	3
Normalized TPT (ms·N·m^{-1})	4.5 ± 1.2	6.6 ± 2.3[a]	**33**	6.3 ± 1.7[b]	9.4 ± 3.7[a,b]	**49**
Normalized HRT (ms·N·m^{-1})	3.5 ± 1.5	4.8 ± 1.4[a]	**39**	5.1 ± 1.4[b]	6.3 ± 1.8[a,c]	**24**
Peak velocity (°·s^{-1})	277.2 ± 21.2	255.1 ± 17.5[a]	**8**	243.3 ± 19.6[b]	230.6 ± 21.2[b]	5
Peak power (W)	309.1 ± 71.9	240.3 ± 62.5[a]	**22**	213.0 ± 53.3[b]	187.7 ± 36.7[b]	12
Peak power load (% MVC)	45.0 ± 7.5	41.7 ± 14.6	7	57 ± 13.8[b]	52.5 ± 10.6[c]	8

Maximal voluntary isometric contraction; MVC, Isokinetic MVC; IsokMVC, optimal angle of plantar flexion during voluntary isokinetic torque production; optimal angle, time to peak twitch torque; TPT and half relaxation time of the electrically evoked twitch; HRT. Bolded % difference values are significant. All values are means ± standard deviations.

[a] Denotes significant differences within groups ($P < 0.05$).

[b] Denotes significant differences between groups ($P < 0.05$).

[c] Denotes a trend ($P = 0.06–0.08$) between age groups.

3.2. Velocity-dependent measures

For the velocity-dependent actions, the young men were ~12% faster for maximum angular velocity, and ~30% more powerful at peak power than the old ($P < 0.05$; Table 1). The young group exhibited ~8% greater peak angular velocity and ~23% greater peak power in the extended compared with the flexed knee position ($P < 0.05$; Table 1). In contrast, there were no statistical differences in peak power and peak velocity between knee angles in the older group (Table 1). Peak power was achieved at a lower % MVC in the extended ($P < 0.05$) and with a trend ($P = 0.08$) at the flexed knee angle for the young compared with old men (Table 1).

At each respective load across the velocity-dependent contractions, the young men produced more torque than the old ($P < 0.05$; Table 2) for both knee angles. The young achieved 7–12% greater angular velocities in the extended than flexed knee at loads $\leq$30% MVC ($P < 0.05$; Fig. 1); whereas there were no detectable differences in velocity between knee angle at the higher relative resistances (i.e., >30% MVC; Fig. 1). In the old men there were no detectable differences in angular velocities across knee angle when compared at each relative load ($P > 0.05$). The young men produced 10–12% greater angular velocities than the older group at 15 and 20% MVC in both knee positions, as well as at 30% MVC in the extended knee, with no other detectable differences (Fig. 1), indicating that at higher loads (i.e., >30% MVC) and slower angular velocities young and old men do not differ.

The young men were 15–32% more powerful in the extended versus flexed knee position across all relative loads ($P < 0.05$; Fig. 2). The old were 22% more powerful in the extended knee for 30% MVC ($P < 0.05$; Fig. 2) with a trend ($P = 0.06$–0.08) for 60 and 75% MVC; whereas no differences were detected for all other loads across knee angles (Fig. 2). Except for 75% MVC for the extended knee, and 60 and 75% MVC in the flexed knee, the young were more powerful than the old at all relative loads in both knee positions ($P < 0.05$; Fig. 2). In the young, peak velocity was shifted with the knee extended from flexion for most relative loads ($P < 0.05$), except for 15 and 45% MVC. However, no detectable differences were found for the older adults (Table 3).

4. Discussion

This study emphasizes that although isometric torque is reduced in both young and old to a similar degree with a flexed knee position, measures of dynamic plantar flexion function between the two age groups are affected differently with changing knee joint position. Specifically, knee angle position had no effect on angular velocity in old men, possibly owing to their age-related diminished maximal angular velocity; whereas the young men were slower in the flexed than extended knee position at lower loads ($\leq$30% MVC which have the higher velocities). Thus, for this synergetic muscle group, young men are more affected by a reduction in the contribution of one muscle pair (i.e., flexing the knee and limiting the contribution of the gastrocnemeii) for velocity-dependent shortening actions than old men. Young men produced their greatest peak power at lower relative MVC values (42–45%) than the older adults (53–57%) in either knee position (Table 1) indicating the older men rely more on the torque component of power during velocity-dependent contractions, possibly due to the age-related intrinsic slowing of their muscles. Our results highlight how age-related alterations specific to individual muscles of a synergistic group can alter the functional capacity of the whole group (triceps surae) thereby requiring different functional strategies from the integrated muscle group to accomplish a certain task.

4.1. Torque generation

The young men were ~25% and ~20% stronger isometrically and isokinetically than the old, respectively, which is typical for this muscle group (Dalton et al., 2009, 2010; Simoneau et al., 2007; Thom et al., 2005; Wakahara et al., 2007). Because voluntary activation capacities (>95%) were similar in the current study and antagonist co-activation and voluntary activation do not seem to play a factor in strength differences in well-practiced younger and older adults (Dalton et al., 2009; Hunter et al., 2008; Klass et al., 2005), a neural activation basis for the age-related reductions in isometric and isokinetic plantar flexor strength seems unlikely. The age-related decrements are likely related to functional and structural alterations at the peripheral level (Hunter et al., 1999; Kaya et al., 2013; Morse et al., 2005; Narici et al., 2008; Thom et al., 2005; Yu et al., 2007).

Novel to our study is that despite a difference in age of ~50 years, isometric (~17%) and slow ($30^\circ\cdot s^{-1}$) isokinetic (~20%) torques had similarly larger values in the extended than in the flexed knee position for both groups (Table 1) despite the old men being weaker and less powerful. In both age groups flexing the knee also resulted in slower evoked contractile properties (Table 1) presumably due to more slack of the musculotendon unit and lesser contractile contribution of the faster gastrocnemius component (Cresswell et al., 1995; Kawakami et al., 1998). The current findings corroborate previous results for young subjects in response to knee flexion (Cresswell et al., 1995; Dalton et al., 2013; Kawakami et al., 1998; Wakahara et al., 2007) and now extend these findings to an older adult model. In young adults, the gastrocnemeii contribute relatively less plantar flexion torque than the soleus, even with the knee extended (~30%) (Fukunaga et al., 1992). Because the function of the gastrocnemeii is compromised to a greater extent than the soleus with adult aging (Fujiwara et al., 2010; Morse et al., 2005), knee flexion did not have a greater effect on the voluntary isometric torque–length relationship of the whole triceps surae in the older men than the young.

In the present study the optimal plantar flexion angle of torque production was unaltered in the older men as a function of knee angle, indicating that peak isokinetic torque occurred at a similar ankle joint angle in an extended than flexed knee. Conversely, the optimal angle of torque production for the young men shifted to a 15% greater plantar flexion angle in the extended versus flexed knee. This indicates that unlike the older men, there was a shift in the plantar flexor dynamic torque–length relationship to longer muscle lengths for the young men. The torque–length relationship governs the torque–velocity

Table 2
Torque (N·m) achieved during each relative load for the velocity-dependent contractions.

	Young (n = 10)			Old (n = 10)		
	Extended	Flexed	% difference	Extended	Flexed	% difference
15% MVC	28.9 ± 5.6	23.8 ± 3.8^{a}	**18**	23.3 ± 2.8^{b}	19.4 ± 2.7^{a,b}	**17**
20% MVC	38.5 ± 7.5	31.8 ± 5.0^{a}	**17**	31.4 ± 3.8^{b}	26.0 ± 3.5^{a,b}	**17**
30% MVC	57.7 ± 11.3	47.7 ± 7.6^{a}	**17**	46.9 ± 5.9^{b}	38.9 ± 5.4^{a,b}	**17**
45% MVC	86.5 ± 17.0	71.5 ± 11.3^{a}	**17**	69.7 ± 8.6^{b}	58.6 ± 8.3^{a,b}	**16**
60% MVC	115.4 ± 22.6	95.4 ± 15.1^{a}	**17**	94.0 ± 11.5^{b}	78.0 ± 10.2^{a,b}	**17**
75% MVC	144.2 ± 28.3	119.2 ± 18.9^{a}	**17**	117.2 ± 14.5^{b}	97.1 ± 13.6^{a,b}	**17**

All values are means ± standard deviations and all % difference values are significant.
[a] Denotes significant differences within groups ($P < 0.05$).
[b] Denotes significant differences between groups ($P < 0.05$).

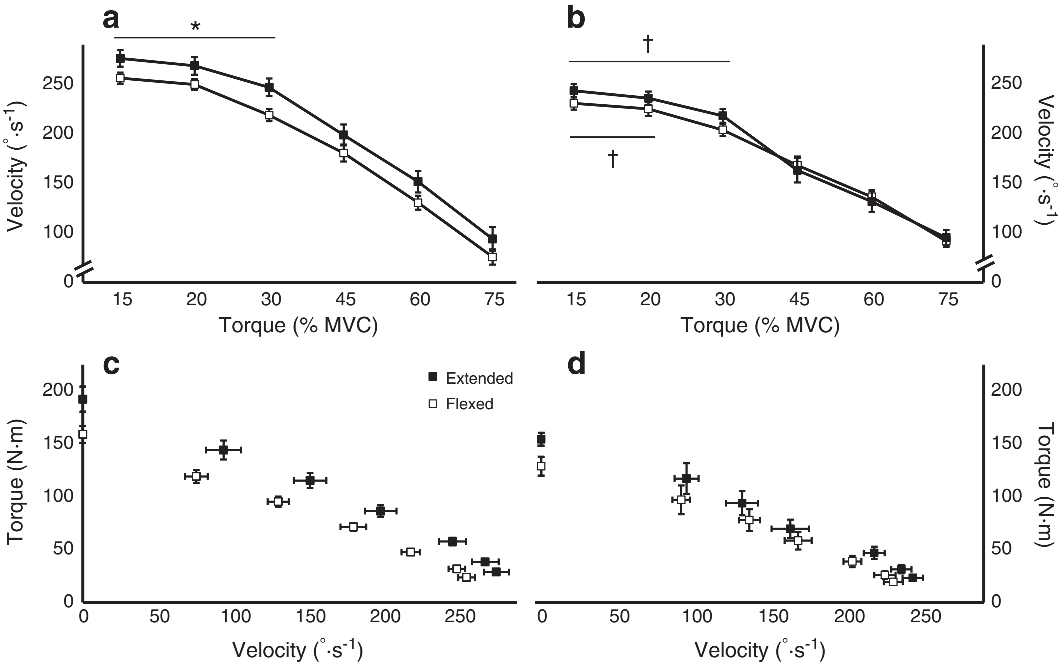

Fig. 1. Voluntary angular velocity for the relative (a,b) and absolute (c,d) plantar flexor torque decreased as the load increased for both age groups. The axes of panels c and d are reversed from panels a and b to be consistent with the typical plotting of a torque–angular velocity relationship. For the young men (a), angular velocity was faster for the lower loads ($P < 0.05$), but was not different at the higher loads in the extended (filled square) than flexed (open square) knee. For the older men (b), there were no detectable differences in angular velocity between knee positions. Panel c highlights a shift down and to the left in the torque–velocity relationship when the knee is flexed to 90° from an extended position (170°) in young, and there was a limited shift in the older men (d). * represents a significant knee angle effect; whereas † indicates a significant difference for age. Values are mean ± SEM.

relationship (Brown et al., 1996) by influencing torque production capacity throughout the functional range of motion. For example, when the knee was flexed from extension, the ankle angle at which peak velocity was attained shifted in the young, but not in the old for the velocity-dependent contractions (Table 3). Even though slow isokinetic and isometric torque generating capacity was not altered differently between age groups from an extended to a flexed knee, age-related disparities in plantar flexor function between the young and old men become evident only at faster velocities when the gastrocnemeii are providing a greater contribution to the movement (see below).

4.2. Angular velocity and power

To exploit the velocity component of power – a critical component of the inherent design and function of skeletal muscle (Lieber and Ward, 2011) – we utilized velocity-dependent contractions. These movements

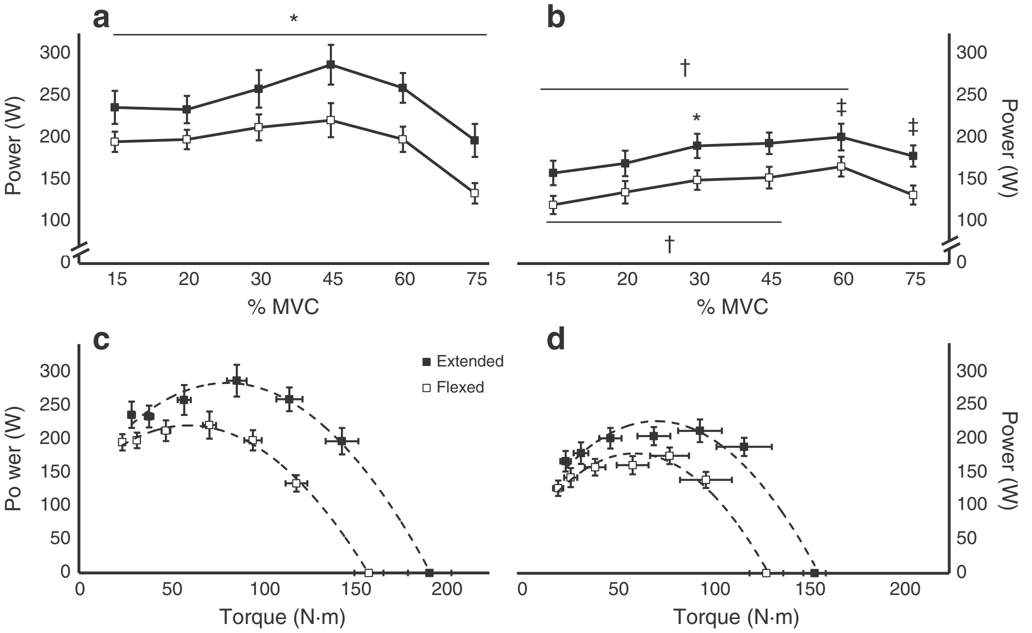

Fig. 2. Plantar flexion power over varying relative (a,b) and absolute (c,d) loads in young (a,c) and old (b,d) men. Power was greater at most relative loads ($P < 0.05$) for the extended (filled square) than flexed (open square) knee position in the young, but not the old. * represents a significant knee angle effect and ‡ represents a trend ($P = 0.06$–0.08) for knee angle; whereas † indicates a significant difference for age. Values are mean ± SEM.

Table 3
Ankle angle (°) at which peak velocity was achieved for the velocity-dependent contractions.

	Young (n = 10)			Old (n = 10)		
	Extended	Flexed	% difference	Extended	Flexed	% difference
15% MVC	9.3 ± 0.7	9.6 ± 0.8	3	9.7 ± 0.6	9.6 ± 0.6	1
20% MVC	9.2 ± 1.8	8.0 ± 2.0[a]	**13**	9.9 ± 0.8	9.2 ± 0.3[b]	7
30% MVC	8.6 ± 2.0	7.5 ± 2.7[a]	**13**	9.6 ± 0.7	9.7 ± 0.4[c]	1
45% MVC	8.8 ± 0.9	8.9 ± 1.6	1	9.1 ± 0.8	9.0 ± 0.5	1
60% MVC	9.5 ± 0.6	8.2 ± 1.6[a]	**14**	8.4 ± 1.5[b]	8.8 ± 1.3	5
75% MVC	9.0 ± 1.4	6.9 ± 2.3[a]	**23**	6.5 ± 1.5[c]	6.6 ± 2.0	2

Bolded % difference values are significant. All values are means ± standard deviations.

[a] Denotes significant differences within groups ($P < 0.05$).

[b] Denotes a trend ($P = 0.06–0.08$) between groups.

[c] Denotes significant differences between groups ($P < 0.05$).

are characterized by maximal effort shortening actions generated as fast as possible against a fixed resistance (i.e., isotonic-like). Unlike isokinetic actions (torque-dependent), the velocity is unconstrained, and therefore voluntary contractile speed of the shortening movement can be assessed. In the present study, the young men exhibited significantly greater angular velocities than the older men, but only at the lighter loads (≤30% MVC). Our results support findings from a study using isokinetic contractions with an extended knee that reported at higher fixed angular velocities older adults experienced greater deficits in torque generating capacity than their younger counterparts (Thom et al., 2005). However, the limitation for studies using isokinetic tests is that older adults are unable to produce reliable maximum torque through a full range of motion for the faster isovelocities, at least for the dorsiflexors and knee extensors (Lanza et al., 2003). Using velocity-dependent contractions we find a strong reliance on the velocity component to achieve peak power in young men; whereas the older men have a greater dependence on torque and slower velocities. This likely represents a compensatory mechanism for the older adults to maintain peak power within a useful operating range of their slower contracting muscle (see Table 1) and more compliant tendons. The current study solidifies previous ideas (Dalton et al., 2010; Thom et al., 2005) that angular velocity is limited for older adults, which is apparent at lighter resistances when velocity is greatest and unconstrained using these isotonic-like contractions.

In contrast to our findings regarding torque generation, age had a differential effect on the relationship between knee angle and the velocity component of power (Fig. 1, Table 1). The young achieved greater angular velocities and peak velocity in the extended versus flexed knee position at lower loads (≤30% MVC), similar to our recent report in young (Dalton et al., 2013). However, unique to the present study was that the older men exhibited no difference in angular velocity detected between knee angle at any load, or at peak velocity (Fig. 1). Muscular power is derived from, and therefore directly influenced by, the torque–angular velocity relationship (Cormie et al., 2011). Thus, the differential effects of knee angle and age between torque and velocity translated into the young exhibiting greater power with the knee extended than flexed over the entire range of relative loads; whereas the older men had limited differences in power production between knee angles. These results indicate a down- and leftward shift in the torque–angular velocity and power curves between young and old men as well as between knee angles (Fig. 2). However, the shift by flexing the knee from an extended position is much more pronounced in the young compared with older men. This suggests an age-related limitation in the optimal torque–length relationship in the flexed knee, a flatter torque–length relationship leading to a blunted torque–angular velocity relationship, or a diminished contribution of the gastrocnemeii. Because older adults have more compliant tendons (Narici et al., 2008) than the young and calcaneal tendon force transmission is reduced with knee flexion (Wakahara et al., 2007) in young adults, these non-contractile factors may also contribute to the age-related disparities in the torque–angular velocity relationship.

The gastrocnemeii contribute ~30% of maximal plantar flexion torque (Fukunaga et al., 1992) and is comprised of ~50% fast twitch motor units (Johnson et al., 1973), but the soleus is only comprised of ~15% fast twitch motor units (Johnson et al., 1973). Faster maximal velocities and shorter contractile times are characteristics of fast twitch muscle fibers, which is reflective of faster cross-bridge cycling and leading to greater peak power than slow twitch fibers (Trappe et al., 2003). Hence, as power is the product of both torque and velocity, the gastrocnemeii can account for almost half (~46%) of the power generating capacity of the triceps surae in young adults (Fukunaga et al., 1992). With adult aging, the gastrocnemeii undergo age-related neuromuscular alterations, whereas soleus neuromuscular properties are better maintained presumably because their sarcopenic response is minimized or delayed in time compared with other limb muscles in human (Dalton et al., 2008, 2009; Fujiwara et al., 2010; Morse et al., 2005) and animal (Deschenes et al., 2010; Moran et al., 2005) models. When the knee is extended from flexion, the velocity capacity of the plantar flexors is enhanced for the young because of the greater contribution available from fast twitch motor units in young men than old. Thus, maximal power is improved to a greater degree in the extended versus flexed knee for the young (22%) when compared with the old (12%).

In summary, our data emphasize the significance of knee joint angle on isometric and dynamic plantar flexion function and how differential effects of aging on each muscle component can result in compensatory strategies among synergists to accomplish the functional task. Specifically, the greater age-related functional impairment of the gastrocnemeii compared with the soleus highlights the reliance of older men on torque generating capacity for power production due to an impaired velocity of contractile function.

Conflict of interest

The authors have no conflicts of interest to disclose.

Acknowledgements

The authors would like to thank all those who volunteered to participate in the experiments, and to acknowledge Justin Paturel and Brianna Cowling for their help with data analysis. This work was supported by the Natural Sciences and Engineering Research Council of Canada. B. H. Dalton is supported by the Michael Smith Foundation for Health Research and the Canadian Institutes of Health Research. M.D. Allen is supported by the Ontario Graduate Scholarship program. G.A. Power is supported by the Alberta Innovates Health Solutions.

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