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ORIGINAL ARTICLE

The genu effect on plantar flexor power

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Abstract Triceps surae function can be modified by changes in knee joint angle through altering the effective contribution of the bi-articular gastrocnemeii. However, the impact on plantar flexor power from altering knee angle has not been studied systematically across a range of loads. Here, in 11 young men (25.7 ± 2.2 years), we determine the effect of knee angle on torque, velocity and power at loads ranging from 15 to 75 % maximal voluntary isometric contraction (MVC). Contractile properties were recorded with either the knee extended (170°) or flexed (90°). Despite similar voluntary activation (~97 %), peak twitch and MVC torques were 25 and 16 % lower in the flexed than extended knee ($P < 0.05$), respectively. Across all loads, subjects were 15–24 % less powerful with the knee flexed than extended ($P < 0.05$). In the flexed knee at relative loads ≤30 % MVC, impaired power was accompanied by 6–9 % slower shortening velocities than the extended knee. However, for the higher loads, limited torque production in the flexed knee was the key factor contributing to the generation of maximal power than for the extended position. This was supported by no change in velocity at higher loads (>30 % MVC) and a 15–22 % lower maximal rate of torque development across all loads. Hence, in a flexed knee position, which disadvantages the contribution of the gastrocnemeii, results in a left-downward shift in the torque–power relationship impairing maximal power production. Thus, the gastrocnemeii are not only a major contributor to plantar flexion torque, but also critical for modifying loaded shortening velocity and ultimately power production.

Keywords Velocity · Strength · Force–velocity · Triceps surae · Dynamic contraction

Abbreviations

HRT	Half relaxation time of twitch
MRTD	Maximal rate of torque development
MVC	Maximal voluntary isometric contraction
SD	Standard deviation
SEM	Standard error of the mean
T–V	Torque–velocity
TPT	Time to peak twitch torque

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Introduction

Muscle power is dependent upon the ability of the muscle to generate torque and speed of contractile shortening. There is an interaction between these two main components in that with increased muscle shortening velocity the probability of cross-bridge formation is reduced; whereas torque production depends highly upon the number of attached cross-bridges (Lieber and Ward 2011). Maximal power is achieved by an optimal combination of shortening velocity and torque generation, and therefore to achieve this, both factors are required to perform at submaximal capacities. Because muscle groups are designed fundamentally to operate at submaximal levels of torque and velocity for optimal function (Lieber and Ward 2011), muscle power may represent a useful indication of muscle mechanics than maximal velocity (Podolin and Ford 1986) or torque alone. However, it is important to understand the relative contributions of torque and velocity on the derivation of power, and thus various studies of muscle mechanics have investigated the torque–velocity (T–V) relationship of muscle and the factors contributing to maximum power generation (Cormie et al. 2011; Lieber and Ward 2011). However, it is unknown how altering the contribution of one muscle in a synergistic muscle group affects the T–V relationship and ultimate power production of the whole group. Thus, we sought to investigate the T–V relationship of two synergistic muscles involved in human plantar flexion, specifically the role of the bi-articular gastrocnemeii in both an optimal (extended knee) and disadvantaged (flexed knee) length–tension relationship on maximal plantar flexion power generation.

The triceps surae contains the lateral and medial gastrocnemius and the soleus, which together are responsible for ~80 % of plantar flexion torque (Cresswell et al. 1995; Murray et al. 1976). All portions of the triceps surae share a common insertion at the calcaneal tendon, yet these muscles exhibit dramatically different anatomical, electrophysiological, histochemical, and functional properties (Tucker et al. 2005 for review). The single joint (ankle) soleus is a habitually active postural muscle that is composed of fewer than 15 % fast twitch motor units, whereas the bi-articular (knee and ankle) gastrocnemeii are less active during stance and are composed of ~50 % fast twitch motor units (Johnson et al. 1973; Joseph and Nightingale 1952; Trappe et al. 2001).

The overall length–tension relationship of the triceps surae can be altered functionally by manipulating the ankle or knee joint angles, or both (Herzog et al. 1991). The gastrocnemius length is affected by both alterations, whereas the soleus length is affected only by changes in ankle angle. When the knee is flexed to 90° from full extension with no change in ankle angle, the gastrocnemeii are placed in a shortened position (Kawakami et al. 1998) resulting in a reduction in plantar flexion maximal voluntary isometric contraction (MVC) torque by ~25 % (Cresswell et al. 1995). This may be caused not only by a mechanical length disadvantage but also due to an increase in motor unit recruitment thresholds (Kennedy and Cresswell 2001) and less total muscle mass involvement with compromised muscle architecture (i.e., pennation angle and fascicle organization) leading to lower tendon force transmission (Wakahara et al. 2007). As a result of these disparities in the same synergistic muscle group, the gastrocnemeii and soleus may work at different torque–length and T–V relationships depending on the knee angle. Therefore, with both synergists contributing optimally to plantar flexion function in the extended knee position, peak power may be reached at higher loads and lower shortening velocities. Conversely, by reducing the contribution of one synergist (i.e., gastrocnemeii) in a flexed knee position, peak power may be achieved at lighter loads and with faster shortening velocities.

Maximal power generation of a muscle (or muscle group) is also influenced by muscle fibre composition (i.e., Type II fibers having a greater capacity to generate torque and faster shortening velocity than Type I) (Fitts and Widrick 1996; Lionikas et al. 2006). Thus, when plantar flexion is tested in an extended versus flexed knee position, maximal power should be greater because the contribution of more fast-type motor units from the gastrocnemius should be enhanced. Indeed, it has been shown that isometric plantar flexion strength is lower when the knee is flexed versus extended (Cresswell et al. 1995; Sale et al. 1982), but isotonic-like angular velocity was faster (Carpentier et al. 1996, 1999). The relative light loads employed (0–6 kg) which were not normalized or adjusted based on knee angle (Carpentier et al. 1996, 1999) resulted in testing only low torques and therefore fast velocities. This may be an unusual situation based on muscle design features (Lieber and Ward 2011), and perhaps did not adequately challenge the weakened bent knee position and therefore velocity was affected minimally by a disadvantaged torque–length relationship of the gastrocnemeii. Testing submaximal loads that are based on relative strengths in each knee position may alter the plantar flexor T–V relationship and as a result, maximum power generation, but this has not yet been explored.

The purpose was to test the power production capacity, with particular emphasis on the velocity component, of the triceps surae over varying and relative resistive loads at two different knee angles: a flexed and extended knee position. Presumably, the bi-articular gastrocnemeii will be placed at a mechanical disadvantage in the flexed knee during the dynamic task. Thus, we hypothesized that the participants will be weaker and slower, and hence less powerful in the flexed compared with the extended knee position owing to less contribution from the disadvantaged gastrocnemeii.

Materials and methods

Participants

Neuromuscular recordings were sampled from the plantar flexors of eleven recreationally and healthy active young men (age: 26.3 ± 3.4 years, height: 178.1 ± 6.1 cm, body mass: 80.1 ± 3.4 kg), who were recruited from the local university population. The local university's ethics review board for experimentation on humans approved the study, which conformed to the Declaration of Helsinki. All participants gave oral and written informed consent prior to the experiments.

Experimental arrangement

Plantar flexion torque, angular velocity and ankle position in the isometric, isokinetic or isotonic mode were recorded using a Biodex System 3 multi-joint dynamometer (Biodex Medical Systems, Shirley, NY). All tests were performed on the dominant (right) leg. Participants performed plantar flexion actions in two knee positions; one with the knee flexed to 90° and the other with the knee extended to 170° (180° extended fully). Participants were seated comfortably in a reclined position with the hip joint at 90° and the ankle at a neutral angle (90°) for isometric contractions and for the starting point of all dynamic shortening plantar flexion contractions. The range of motion of the ankle for the dynamic contractions was set to 30° (neutral to 30° of plantar flexion). The foot was secured to the footplate using a custom-made binding at the ankle and two Velcro straps across the toes and dorsum of the foot. During all contractions, the participants were secured to the Biodex chair with inelastic straps around the shoulders and waist. To minimize involvement of the thigh muscles, a thigh support with an inelastic strap was used for stabilization of the limb. The ankle joint was aligned with the axis of rotation of the dynamometer. Plantar flexor torques, velocities and positions were sampled at 100 Hz using a 12-bit analog-to-digital converter (Power 1401; Cambridge Electronic Design, Cambridge, UK) and digitized online using Spike2 software (Cambridge Electronic Design).

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 bar electrode was held firmly in the distal portion of the popliteal fossa between the origins of the heads of the gastrocnemius to stimulate the tibial nerve.

Experimental procedures

Data were collected during one visit to the neuromuscular laboratory, in which participants performed isometric and dynamic shortening contractions at the two different knee angles. The order of knee angle testing was assigned pseudo-randomly, but the procedures were performed in an identical sequence as outlined below. Testing sessions for each knee angle were separated by at least 20 min to account for any fatigue accumulation.

To first evoke plantar flexor twitches at rest, the current was increased gradually until the amplitude of the twitch peaked with no further enhancement in amplitude from increasing current. To ensure full activation of all motor axons, the current was set 10–15 % higher than the plateau level. Following the electrically evoked contractions, participants attempted three ~6–8 s isometric MVCs. An additional MVC was performed if the first three varied in peak torque amplitude by more than 5 %. Each MVC effort included a supramaximal twitch delivered ~1 s prior (at rest), another during the peak of MVC torque (T_s) and one more ~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 {% activation = $[1-(T_s/T_r)] \times 100$} (Todd et al. 2004). Participants were encouraged verbally during all maximal voluntary isometric and dynamic efforts and provided visual feedback on a computer monitor. All isometric MVCs were separated by at least 3 min of rest.

Three min following the MVC attempts, the participants were familiarized with the maximal effort slow isokinetic (30° s^{-1}) shortening contractions by performing 3–5 consecutive attempts separated by ~1 s. These contractions are dependent upon maximal torque production of a participant at a pre-set velocity. Upon completion of a slow isokinetic contraction, and with the plantar flexors relaxed, the dynamometer was returned (~1 s) to the 90° starting position (neutral) by the investigator. Following 3 min rest, the participant performed two isokinetic attempts with the higher of two torque values used in analysis.

Next (following another 3 min rest period), 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). During these dynamic efforts, participants were instructed to move the dynamometer "as fast and as hard as possible" and were provided verbal encouragement. Visual feedback of the velocity profile was displayed on a computer monitor. Once a shortening contraction was completed, the dynamometer returned the foot passively to the original starting position (neutral ankle angle) at a speed of ~60° s^{-1}. Familiarization involved five dynamic contractions separated by short rest intervals of ~5–10 s with a resistance of 20 % MVC. These contractions have been shown to be reliable day-to-day (Power et al. 2011), and 20 % MVC represents a moderate load for this type of contraction (Dalton et al. 2010, 2012). This portion of the session was followed by 3 min of rest.

Finally, the participants performed pairs of unconstrained velocity shortening contractions (isotonic mode) with which to construct a torque–velocity relationship at six different loads (15, 20, 30, 45, 60, and 75 % MVC). Because MVC amplitudes were lower in the flexed compared with the extended knee, the imposed loads were normalized to the respective isometric MVC value for the two knee angles. Each pair of contractions was separated by 30 s of rest. These contractions were assigned in random order to ensure fatigue was not a factor. All subjects were initially unaware of the load (i.e., resistance) set for the velocity-dependent contractions, but were instructed to move the load "as hard and as fast as possible throughout the entire range of motion". To ensure a maximal effort, all participants were provided verbal encouragement and visual feedback of the velocity profile on a computer monitor.

Data analysis and statistics

Electrically evoked isometric contractile function of the plantar flexors was assessed by measuring peak twitch torque (N·m), time to peak twitch torque (TPT; ms) and half relaxation time (HRT; ms) of the twitch. All voluntary and evoked isometric values were taken from the maximum amplitude of the recording. Dynamic torque, power and maximum rate of torque development (MRTD, $N{\cdot}m{\cdot}s^{-1}$) were measured from the maximum torque value for the isokinetic actions. Shortening velocity, power and MRTD of the unconstrained velocity task (isotonic mode) were taken from each of the six relative load conditions; for each pair, the contraction with the faster peak velocity was used in analysis. For the isokinetic task, power (W) was calculated as the product of the peak torque generated by the participant (N·m) and the pre-set velocity (rad s^{-1}) of the dynamometer. For the unconstrained velocity movements, power (W) was calculated as the product of voluntary generated shortening velocity (rad s^{-1}) and voluntary torque that attained the greatest instantaneous power value for each pre-set external load (N·m) of the dynamometer. Peak power during the six loaded velocity-dependent contractions was determined as the optimal torque and velocity which produced the highest value across the six loads. Further, the position at which instantaneous peak velocity occurred was analyzed for an effect of knee angle across the various loads.

Data were analyzed using SPSS version 17 (SPSS, Chicago, IL). Paired *t* tests were performed to analyze all isometric and isokinetic data for an effect of joint angle, except for voluntary activation in which a non-parametric Mann–Whitney *U* test was used. A two-way analysis of variance (knee angle × load) was used to analyze all data from the velocity-dependent contractions. The α level was set at $P \leq 0.05$. To explore significant main effects and interactions a Tukey's HSD post hoc analysis was utilized. Descriptive statistics are reported as means ± standard deviations (SDs) in the text and tables and mean ± standard error of the mean (SEM) in the figures.

Results

Isometric and isokinetic measures

Despite similar and high voluntary activation ($P = 0.42$) between knee angles, isometric MVC and isokinetic peak torque was 16 % ($P < 0.01$) and 18 % ($P < 0.05$) lower in the flexed compared with extended knee, respectively (Table 1). Voluntary MRTD during the MVC was 27 % slower in the flexed than extended knee ($P < 0.01$), but not different between knee angles for the slow isokinetic task ($P = 0.15$; Table 1). Peak twitch torque was 25 % ($P < 0.01$) lower and TPT was 7 % slower ($P < 0.01$) in the flexed compared with the extended knee position, but no difference existed for half relaxation time of the twitch ($P = 0.54$) between knee angles.

Velocity-dependent measures

Due to the weaker MVC values in the flexed knee position compared with extended, the imposed torque loads for the velocity-dependent contractions were lower in the flexed knee (Table 2; $P < 0.05$). For both knee angles, shortening velocity became progressively faster as the load decreased (Figs. 1, 2). At lighter loads, shortening velocity was 6–9 % slower with the knee flexed than extended (15–30 % MVC; $P < 0.05$), with no differences at the heavier loads ($P = 0.13$) and no detectable differences between knee angle in the position at which peak velocity occurred at any relative load ($P = 0.12$). However, power was 15–24 % less at all relative loads in the flexed than the extended knee (Fig. 3a; $P < 0.05$). Thus, there was a downward and leftward shift in the torque–power relationship for the flexed compared with the extended knee (Fig. 3b). Peak power occurred at 45 % MVC for both knee positions (Table 1). The reduced power in the flexed than extended knee was accompanied by 15–22 % slower MRTD during the velocity-dependent contractions at all loads (Fig. 4).

Because torque values were lower for all relative loads during the flexed knee than the extended condition (Table 2), we also analyzed and compared absolute loads that were similar (Table 3) at the two different knee positions: a low load (15 % MVC for extended and 20 % MVC for flexed, $P = 0.33$) and a high load (60 % MVC for extended and 75 % MVC for flexed, $P = 0.69$). When the loads were equated, shortening velocity was 9 and 47 %

Table 1 Neuromuscular properties of the plantar flexors for two knee angles

Group ($n = 11$)	Extended	Flexed
MVC (N·m)	203.5 ± 56.3	170.1 ± 39.8*
Voluntary activation (%)	97.0 ± 1.5	96.4 ± 2.6
MVC MRTD (N·m·s^{-1})	684.3 ± 228.8	502.8 ± 159.7*
IsokMVC (N·m)	133.4 ± 36.9	109.9 ± 23.4*
IsokMVC MRTD (N·m·s^{-1})	1144.7 ± 283.3	953.3 ± 214.3
Peak twitch torque (N·m)	29.6 ± 8.9	22.2 ± 7.0*
Time to peak twitch (ms)	121.0 ± 20.1	129.3 ± 15.1*
Half relaxation time (ms)	88.0 ± 21.5	91.4 ± 16.3
Peak velocity (° s^{-1})	278.8 ± 27.4	258.6 ± 18.0*
Peak power (W)	297.6 ± 76.8	242.6 ± 75.4*
Torque at peak power (N·m)	87.4 ± 19.0	75.1 ± 16.4*
Peak power load (% MVC)	45	45

MVC maximal voluntary isometric contraction, *MRTD* maximal rate of torque development, *IsoKMVC* isokinetic maximal voluntary contraction

For the flexed knee (170°), voluntary and electrically evoked properties of the plantar flexors were weaker, and slower (*$P < 0.05$) than for the extended knee (90°) even though voluntary activation and half relaxation time were similar at both joint angles. Hence, peak power was less for the flexed than extended knee (*$P < 0.01$). Values are mean ± SD

Table 2 Relative pre-set loads for the velocity-dependent contractions

Group ($n = 11$)	Extended	Flexed
15 % MVC	30.5 ± 8.4	25.5 ± 6.0*
20 % MVC	40.7 ± 11.0	34.0 ± 8.0*
30 % MVC	61.1 ± 15.8	51.0 ± 11.9*
45 % MVC	91.6 ± 25.3	76.5 ± 17.9*
60 % MVC	122.1 ± 33.8	102.1 ± 23.9*
75 % MVC	152.6 ± 42.2	127.6 ± 29.8*

Absolute pre-set torque values were less in the flexed compared with the extended knee position (*$P < 0.05$) for all relative loads. Values are mean ± SD

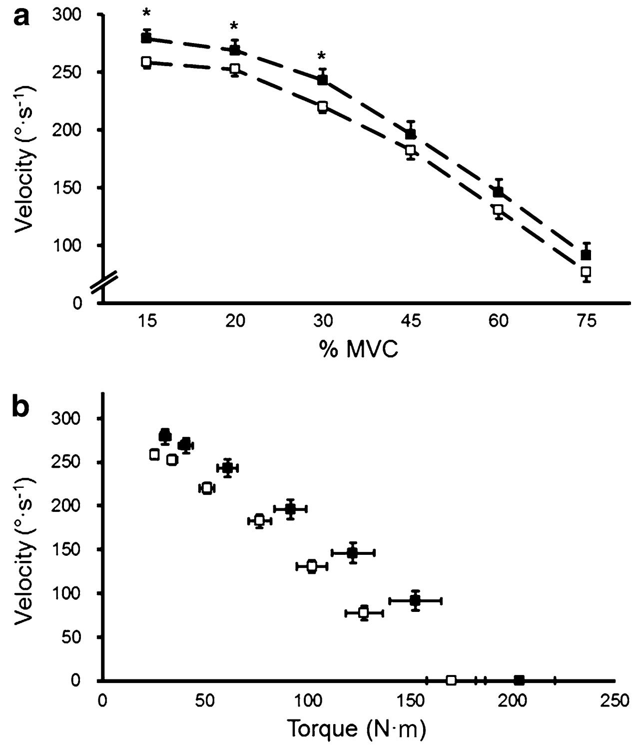

Fig. 2 Voluntary shortening velocity for the relative (**a**) and absolute (**b**) loads decreased progressively as the load increased. Shortening velocity was faster for the lower loads (*$P < 0.05$), but was not different at the higher loads in the extended (*filled*) than flexed (*open*) knee. Panel **b** 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°). Values are mean ± SEM

slower (Table 3) in the flexed than the extended knee for the low ($P < 0.05$) and high ($P < 0.01$) loads, respectively. However, peak velocity occurred at a similar position in plantar flexion range of motion (~9.2°) for the low load ($P = 0.34$), but was achieved slightly earlier during plantar flexion excursion in the flexed (5.3 ± 1.4°) than extended knee (7.6 ± 1.6°; $P < 0.01$) for the high load, which might further support a shift in the torque–length relationship. Power was not different between knee angles for the low load ($P = 0.95$), but 41 % less ($P < 0.01$) in the flexed compared with the extended for

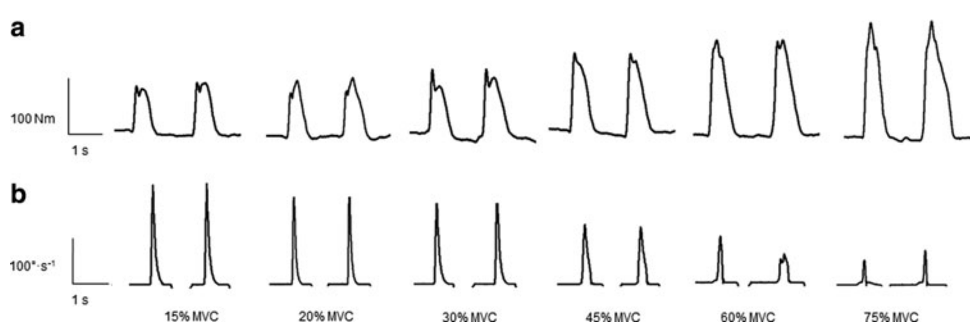

Fig. 1 Representative unprocessed data taken from one subject for the velocity-dependent contractions at varying relative loads of maximal voluntary isometric contraction (% MVC) with an extended (170°) knee position. The torque (**a**) output increased as the load increased, while velocity (**b**) decreased

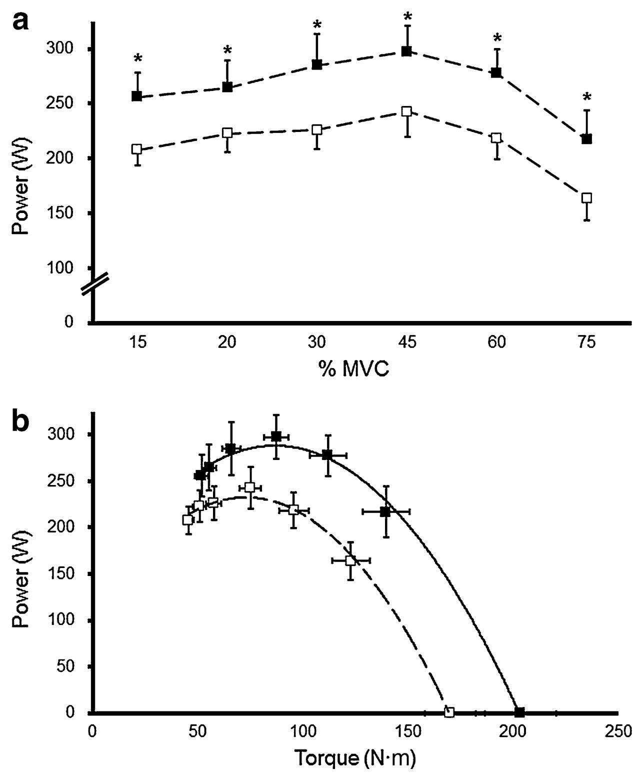

Fig. 3 Power values over varying relative (**a**) and absolute (**b**) loads. Power was greater at all relative loads (*$P < 0.01$) for the extended (*filled*) than flexed (*open*) knee position. Panel **b** shows a shift down and to the left in the torque–power relationship when the knee is flexed to 90° compared with an extended position (170°). Values are mean ± SEM

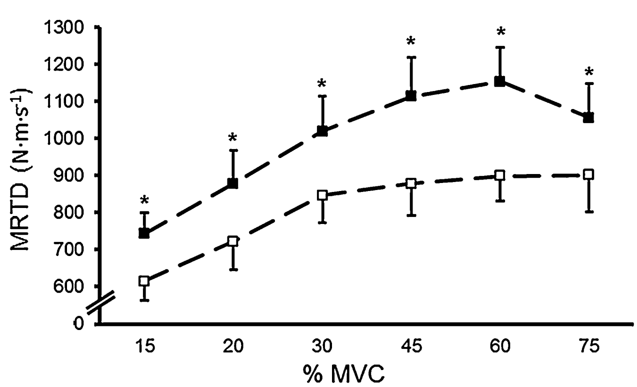

Fig. 4 Maximal rate of torque development (MRTD) for the velocity-dependent contractions. MRTD was greater in the extended (*filled*) compared with the flexed (*open*) knee position at all relative loads (*$P < 0.05$). Values are mean ± SEM

the high load (Table 3). The reduced power was accompanied by a 22 % lower ($P < 0.05$) MRTD in the flexed than extended knee for the high load, but there were no detectable knee angle differences in MRTD for the low load (Table 3).

Discussion

By shortening the gastrocnemeii with a flexed knee, previous studies reported reductions in isometric MVC torque generation than an extended knee (Cresswell et al. 1995; Sale et al. 1982), but in other studies shortening velocity against very light loads was faster in the flexed knee position (Carpentier et al. 1996, 1999). From these disparate findings, it was not known how these apparent divergent alterations in torque and velocity would affect power production, or whether shortening velocity would continue to be faster in the flexed knee position when moderate to heavy loads are imposed compared with the extended knee position. Results from the present study indicate that plantar flexor isometric and slow (30° s^{-1}) isokinetic torque generation capacity is indeed reduced when the knee is flexed, but remarkably we also found an attenuation of shortening velocity in this position with moderate loads than in the extended knee. While power production is highly dependent upon the T–V relationship, the torque–length relationship dictates the capacity of the muscle to generate optimal torque (Brown et al. 1996). Thus, altering the length of the gastrocnemeii, by flexing the knee, plays a critical role in the development of maximal plantar flexion power.

Torque generation

Despite high voluntary activation levels (~97 %) for both knee angle positions, torque was 16, 25, and 18 % weaker in the flexed compared with extended knee for the voluntary and electrically evoked isometric and slow isokinetic (30° s^{-1}) contractions, respectively. These reductions in isometric and isokinetic plantar flexor torques are in line with earlier reports (Cresswell et al. 1995; Fugl-Meyer et al. 1979; Sale et al. 1982; Wakahara et al. 2007). Furthermore, we found that the compromised isometric torque production capacity in the flexed knee was accompanied by a 27 % slower MRTD than the extended knee. This impairment in rapid isometric torque generation may reflect a limitation of the plantar flexors to perform quick dynamic contractions against moderate to heavy resistances in the flexed knee position. Our current observations can likely be explained by a mechanical disadvantage due to a shift towards higher MU recruitment thresholds (Kennedy and Cresswell 2001; Nishimura and Nakajima 2002), mechanical restrictions of the contractile apparatus (Herzog et al. 1991; Kawakami et al. 1998; Wakahara et al. 2007), and impairments in neuromuscular propagation and activation (Arampatzis et al. 2006; Cresswell et al. 1995) of the gastrocnemeii, or alterations in the whole muscle–tendon unit torque–length relationship (Arampatzis et al. 2006) when the knee is flexed. Because the torque–length

Table 3 Velocity-dependent values at a low and high load

Group ($n = 11$)	Low load		High load	
	Extended	Flexed	Extended	Flexed
Load (N·m)	30.5 ± 8.4	34.0 ± 8.0	122.1 ± 33.8	127.6 ± 29.8
Torque (N·m)	51.79 ± 10.8	50.8 ± 9.8	112.0 ± 28.7	122.7 ± 29.7
Velocity (° s^{-1})	278.8 ± 27.4	252.4 ± 18.8*	146.1 ± 37.5	77.0 ± 26.9*
Power (W)	255.9 ± 75.1	226.14 ± 58.9	277.7 ± 72.4	163.9 ± 68.1*
MRTD (N·m·s^{-1})	742.4 ± 190.6	721.7 ± 246.9	1153.4 ± 301.2	901.6 ± 329.4*

We analyzed similar absolute resistances (Load) at the two knee angles: a low load (15 % MVC for extended and 20 % MVC for flexed, $P = 0.33$) and a high load (60 % MVC for extended and 75 % MVC for flexed, $P = 0.69$). When resistances were equated at a low and high load, peak velocity (Velocity) was slower in the flexed than extended knee (*$P < 0.05$). However, peak power and maximal rate of torque development (MRTD) were less in the flexed knee only for the high load (*$P < 0.05$). Voluntary torque production (Torque) at peak power was not significantly different between knee angles for the low ($P = 0.96$) and high ($P = 0.30$) loads. Values are mean ± SD

relationship indeed interacts with the torque–velocity relationship (Brown et al. 1996), the aforementioned mechanical disadvantage may contribute to impairments in, not only torque, but also velocity. For example, in the present study, there was a shift in the position at which peak velocity was attained at the varying knee angles for the high absolute load.

Velocity

Unique to our experiment was the finding that voluntary shortening velocity was 6–9 % slower for the flexed than extended knee at relative loads ≤30 % MVC (Fig. 2). This is in contrast to reports on maximal effort isovelocity contractions at moderate to fast (180–350° s^{-1}) speeds (Fugl-Meyer et al. 1979; Svantesson et al. 1991; Wakahara et al. 2007). For example, Svantesson et al. (1991) showed that maximal plantar flexion dynamic torque at a constrained velocity of 240° s^{-1} was similar for a knee angle flexed to 90° compared with an extended knee. However, isovelocity contractions are dependent on the ability of the participant to generate torque when angular velocity is fixed. Because angular velocity is constrained artificially and absolute velocities are used to compare across conditions, it is challenging to determine the effect of velocity on power production. Conversely, when torque is constant and velocity can vary freely, the muscle–tendon unit functions more closely to in vivo conditions and changes in shortening velocity can be assessed (Dalton et al. 2010, 2012; Power et al. 2010).

Two studies (Carpentier et al. 1996, 1999) using "isotonic-like" shortening contractions concluded that the greatest maximal plantar flexion velocities against light absolute resistances (0–6 kg) were achieved with the knee flexed to 90° (range 515 ± 124° s^{-1}–765 ± 128° s^{-1}) than extended fully (range 423 ± 74° s^{-1}–551 ± 124° s^{-1}). Although these studies do not support other reports (see above), it was suggested that the greater angular velocities achieved in the flexed knee position were due to an optimal position of the gastrocnemius muscle heads in terms of their torque–length and T–V relationships (Carpentier et al. 1996). However, it is disadvantageous for a muscle designed for a habitual task to operate at unusually high shortening velocities, because the relative torque generated would be low (Lieber and Ward 2011). Furthermore, those reports based on isometric torque generation (Cresswell et al. 1995; Sale et al. 1982) suggest the torque–length relationship is suboptimal in the flexed than extended knee. Thus, the present study investigated shortening velocity over a range of relative and absolute submaximal loads that more closely relate to the functional design of the plantar flexor muscle group. Our results indicate that plantar flexion velocity was slower for moderate relative loads (<30 % MVC; Table 2) and indeed 9 and 47 % slower for low (~32 N·m) and heavy (~125 N·m) absolute loads, respectively, in the flexed versus extended knee. Thus, even when the resistances were equated for an absolute load, shortening velocity was significantly slower for the flexed than extended knee (Table 3).

Plantar flexion velocity may have been reduced for the flexed versus extended knee in the present study for a number of reasons. First, because the soleus represents an architectural design that is developed primarily for isometric strength capacity and not velocity, as determined by its modest mass (275 g), short muscle fibres (Ward et al. 2009), and high proportion of type I muscle fibers (Johnson et al. 1973; Trappe et al. 2001), disadvantaging the relatively faster contracting gastrocnemius and emphasizing a greater relative contribution from the soleus in the flexed than extended knee may reduce shortening velocity in the current experiment. Second, the capacity of the intrinsic mechanical structures of the gastrocnemeii to achieve high velocities under moderate to high loads may have been impaired with a flexed knee position. Indeed, a report by Wakahara et al. (2007) showed that muscle fascicle shortening velocities were 40 and 56 % slower in the flexed than extended knee, respectively, when subjects performed maximal effort plantar flexion actions against constrained angular isovelocities of 30 and 350° s^{-1}. Third, muscle fiber segments that achieve higher velocities have been found consistently to have a greater curvature with respect to the T–V relationship (Faulkner et al. 1982; Widrick et al. 1998). Because the plantar flexors are capable of higher velocities against 'unloaded' to light resistances in the flexed than extended knee (Carpentier et al. 1996, 1999), presumably, the curvature of the T–V relationship of the muscle fibres is much greater in the flexed knee than the flatter curvature in the extended knee position. We observed that shortening velocities were lower in the flexed than extended knee at moderate loads (<30 % MVC), but similar for the higher relative loads. Thus, the greater maximal velocities reported for unloaded (Carpentier et al. 1996) and light loads (<6 kg) (Carpentier et al. 1999) in the flexed versus extended knee may be lost when a moderate to heavier load is imposed during dynamic shortening actions similar to that used in the present study.

Power

Previous studies have not explored systematically the effect of knee angle on plantar flexor power. Maximal power is driven by an optimal relationship between torque and velocity and in our study, isometric strength and shortening velocity (Tables 2, 3; Fig. 2) were both reduced in the flexed compared with extended knee. Hence, power was reduced by 15–24 % for all relative loads (Fig. 3) and these reductions were accompanied by a 15–22 % lower MRTD for the velocity-dependent contractions in the flexed knee position (Fig. 4). Performance of dynamic muscle actions may also be dependent upon ballistic torque production, or MRTD, the ability to generate torque rapidly (Andersen and Aagaard. 2006). For the moderate relative loads (≤30 % MVC) in our study, slower contractile speeds seem to be a critical factor for the lower power produced in the flexed than extended knee as both velocity and MRTD were lower in the flexed knee. As the load increased, MRTD remained lower in the flexed than extended knee, but velocity was similar. Thus, contractile speed had a lesser impact on power for the heavier loads; whereas maximal torque generation capacity seemed to have a greater influence upon the heavier loaded dynamic shortening actions. Because flexing the knee places the gastrocnemius muscle fascicles in a shortened, suboptimal position (Kawakami et al. 1998), isometric (Cresswell et al. 1995) and slow isokinetic (Wakahara et al. 2007) torque is reduced compared with an extended knee. In the present study, the flexed knee limited the force-generators of the gastrocnemius and resulted in an inability to generate torque rapidly, ultimately, impairing power production.

Muscular power is dependent upon and limited by the T–V relationship of the whole muscle–tendon unit (Cormie et al. 2011). In the current study, we observed a left and downward shift in T–V relationship (Fig. 2), and this led to a left and downward shift in the torque-power curve for the flexed than extended knee (Fig. 3). Hence, power was reduced at all relative loads. Furthermore, the gastrocnemius contributes 30–40 % of plantar flexion torque during isometric MVC (Cresswell et al. 1995; Fukunaga et al. 1992) and is composed of ~50 % fast twitch motor units (Johnson et al. 1973); whereas the soleus is composed of only ~15 % fast twitch motor units (Johnson et al. 1973; Trappe et al. 2001). Characteristic of fast twitch muscle fibers is higher maximal velocities and shorter electrically evoked contraction times, which allows for faster cross-bridge cycling than slow twitch muscle fibers (Bottinelli et al. 1991; Fitts and Widrick 1996), and thus greater peak power (Trappe et al. 2003). Essentially, by flexing the knee, the plantar flexors have a greater relative contribution from slow twitch motor units towards power production, and thus have a lower capacity for maximal power in the flexed versus extended knee as the fast twitch motor units of the gastrocnemeii have a more limited contribution compared with the soleus. Furthermore, tendon compliance may play a role in our knee angle comparisons for the isometric and slow isovelocity actions. Because the majority of the muscle–tendon length changes during concentric-only movements are due to fascicle shortening (Kawakami et al. 2002) and simulated alterations in tendon stiffness have little effect on plantar flexion moment–angle curves for isokinetic contractions (Bobbert and van Ingen Shenau 1990), tendon properties should not be a significant factor when comparing across knee angles for the fast velocity-dependent actions.

Regardless of the origin of the limitations in plantar flexion power generation for a flexed versus extended knee, our data emphasize the critical importance of knee joint angle in dynamic plantar flexion performance. In an extended knee, the gastrocnemeii operate with relatively longer fascicle lengths and their relatively greater percentage of fast twitch motor units are able to contribute more to generate greater power during rapid movements against moderate to heavy resistances than in the flexed knee position.

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Ethical standards The experiments comply with the current laws of the country in which they were performed.

Conflict of interest The authors declare they have no conflict of interest.

References

Andersen LL, Aagaard P (2006) Influence of maximal muscle strength and intrinsic muscle contractile properties on contractile rate of force development. Eur J Appl Physiol 96:46–52

Arampatzis A, Karamanidis K, Stafilidis S, Morey-Klapsing G, DeMonte G, Bruggemann GP (2006) Effect of different ankle- and knee-joint positions on gastrocnemius medialis fascicle length and EMG activity during isometric plantar flexion. J Biomech 39:1891–1902

Bobbert MF, van Ingen Shenau GJ (1990) Isokinetic plantar flexion: experimental results and model calculations. J Biomech 23:105–119

Bottinelli R, Schiaffino S, Reggiani C (1991) Force–velocity relations and myosin heavy chain isoform compositions of skinned fibres from rat skeletal muscle. J Physiol 437:655–672

Brown IE, Scott SH, Loeb GE (1996) Mechanics of feline soleus: II design and validation of a mathematical model. J Muscle Res Cell Motil 17:207–219

Carpentier A, Duchateau J, Hainaut K (1996) Velocity-dependent muscle strategy during plantarflexion in humans. J Electromyogr Kinesiol 6:225–233

Carpentier A, Duchateau J, Hainaut K (1999) Load-dependent muscle strategy during plantarflexion in humans. J Electromyogr Kinesiol 9:1–11

Cormie P, McGuigan MR, Newton RU (2011) Developing maximal neuromuscular power: part 1-biological basis of maximal power production. Sports Med 41:17–38

Cresswell AG, Löscher WN, Thorstensson A (1995) Influence of gastrocnemius muscle length on triceps surae torque development and electromyographic activity in man. Exp Brain Res 105:283–290

Dalton BH, Power GA, Vandervoort AA, Rice CL (2010) Power loss is greater in old men than young men during fast plantar flexion contractions. J Appl Physiol 109:1441–1447

Dalton BH, Power GA, Vandervoort AA, Rice CL (2012) The age-related slowing of voluntary shortening velocity exacerbates power loss during repeated fast knee extensions. Exp Gerontol 47:85–92

Faulkner JA, Claflin DR, McCully KK, Jones DA (1982) Contractile properties of bundles of fiber segments from skeletal muscles. Am J Physiol 243:C66–C73

Fitts RH, Widrick JJ (1996) Muscle mechanics: adaptations with exercise-training. Exerc Sport Sci Rev 24:427–473

Fugl-Meyer AR, Sjöström M, Wählby L (1979) Human plantar flexion strength and structure. Acta Physiol Scand 107:47–56

Fukunaga T, Roy RR, Shellock FG et al (1992) Physiological cross-sectional area of human leg muscles based on magnetic resonance imaging. J Orthop Res 10:928–934

Herzog W, Read LJ, ter Keurs HEDJ (1991) Experimental determination of force–length relations of intact human gastrocnemius muscles. Clin Biomech 6:230–238

Johnson MA, Polgar J, Weightman D, Appleton D (1973) Data on the distribution of fibre types in thirty-six human muscles. An autopsy study. J Neurol Sci 18:111–129

Joseph J, Nightingale A (1952) Electromyography of muscles of posture: leg muscles in males. J Physiol 117:484–491

Kawakami Y, Ichinose Y, Fukunaga T (1998) Architectural and functional features of human triceps surae muscles during contraction. J Appl Physiol 85:398–404

Kawakami Y, Muraoka T, Ito S, Kanehisa H, Fukunaga T (2002) In vivo muscle fibre behaviour during counter-movement exercise in humans reveals a significant role for tendon elasticity. J Physiol 540:635–646

Kennedy PM, Cresswell AG (2001) The effect of muscle length on motor-unit recruitment during isometric plantar flexion in humans. Exp Brain Res 137:58–64

Lieber RL, Ward SR (2011) Skeletal muscle design to meet functional demands. Philos Trans R Soc Lond B Biol Sci 366: 1466–1476

Lionikas A, Li M, Larsson L (2006) Human skeletal muscle myosin function at physiological and non-physiological temperatures. Acta Physiol 186:151–158

Murray MP, Guten GN, Baldwin JM, Gardner GM (1976) A comparison of plantar flexion torque with and without the triceps surae. Acta Orthop Scand 47:122–124

Nishimura Y, Nakajima Y (2002) Effect of muscle length on the recruitment property of single motor units in humans. Neurosci Lett 332:49–52

Podolin RA, Ford LE (1986) Influence of partial activation on force-velocity properties of frog skinned muscle fibers in millimolar magnesium ion. J Gen Physiol 87:607–631

Power GA, Dalton BH, Rice CL, Vandervoort AA (2010) Delayed recovery of velocity-dependent power loss following eccentric actions of the ankle dorsiflexors. J Appl Physiol 109:669–676

Power GA, Dalton BH, Rice CL, Vandervoort AA (2011) Reproducibility of velocity-dependent power: before and after lengthening contractions. Appl Physiol Nutr Metab 36:626–633

Sale D, Quinlan J, Marsh E, McComas AJ, Belanger AY (1982) Influence of joint position on ankle plantarflexion in humans. J Appl Physiol 52:1636–1642

Svantesson U, Ernstoff B, Bergh P, Grimby G (1991) Use of a Kin-Com dynamometer to study the stretch-shortening cycle during plantar flexion. Eur J Appl Physiol Occup Physiol 62:415–419

Todd G, Gorman RB, Gandevia SC (2004) Measurement and reproducibility of strength and voluntary activation of lower-limb muscles. Muscle Nerve 29:834–842

Trappe SW, Trappe TA, Lee GA, Costill DL (2001) Calf muscle strength in humans. Int J Sports Med 22:186–191

Trappe S, Gallagher P, Harber M, Carrithers J, Fluckey J, Trappe T (2003) Single muscle fibre contractile properties in young and old men and women. J Physiol 552:47–58

Tucker KJ, Tuncer M, Turker KS (2005) A review of the H-reflex and M-wave in the human triceps surae. Hum Mov Sci 24:667–688

Wakahara T, Kanehisa H, Kawakami Y, Fukunaga T (2007) Fascicle behavior of medial gastrocnemius muscle in extended and flexed knee positions. J Biomech 40:2291–2298

Ward SR, Eng CM, Smallwood LH, Lieber RL (2009) Are current measurements of lower extremity muscle architecture accurate? Clin Orthop Relat Res 467:1074–1082

Widrick JJ, Norenberg KM, Romatowski JG et al (1998) Force-velocity-power and force-pCa relationships of human soleus fibers after 17 days of bed rest. J Appl Physiol 85:1949–1956