

Built for speed: musculoskeletal structure and sprinting ability

Sabrina S. M. Lee¹ and Stephen J. Piazza^{1,2,3,*}

Departments of ¹Kinesiology, ²Mechanical Engineering and ³Orthopaedics and Rehabilitation, The Pennsylvania State University, University Park, PA 16802, USA

*Author for correspondence at present address: 29 Recreation Building, University Park, PA 16802, USA (piazza@psu.edu)

Accepted 17 August 2009

SUMMARY

The musculoskeletal structure of the foot and ankle has the potential to influence human sprinting performance in complex ways. A large Achilles' tendon moment arm improves the mechanical advantage of the triceps surae but also produces larger shortening velocity during rapid plantarflexion, which detracts from the force-generating capacity of the plantarflexors. The lever arm of the ground reaction force that resists the muscular plantarflexor moment during propulsive push-off is constrained in part by the skeletal structure of the foot. In this study, we measured the plantarflexion moment arms of the Achilles' tendon, lateral gastrocnemius fascicle lengths and pennation angles, and anthropometric characteristics of the foot and lower leg in collegiate sprinters and height-matched non-sprinters. The Achilles' tendon moment arms of the sprinters were 25% smaller on average in sprinters than in non-sprinters ($P<0.001$) whereas the sprinters' fascicles were 11% longer on average ($P=0.024$). The ratio of fascicle length to moment arm was 50% larger in sprinters ($P<0.001$). Sprinters were found to have longer toes ($P=0.032$) and shorter lower legs ($P=0.026$) than non sprinters. A simple computer simulation of the sprint push-off demonstrated that shorter plantarflexor moment arms and longer toes, like those measured in sprinters, permit greater generation of forward impulse. Simulated propulsion was enhanced in both cases by increasing the 'gear ratio' of the foot, thus maintaining plantarflexor fibre length and reducing peak fibre shortening velocity. Longer toes especially prolonged the time of contact, giving greater time for forward acceleration by propulsive ground reaction force.

Key words: anthropometry, moment arm, muscle architecture, plantarflexors, sprinting, toes.

INTRODUCTION

The ability to accelerate rapidly during the first few strides of a 100 m race is what separates truly elite human sprinters from merely good ones (Baumann, 1976; Hunter et al., 2005). During the push off from the starting blocks and in the several steps that follow, the leg muscles of a sprinter must do as much concentric work as possible in a coordinated fashion to increase the forward velocity of the body's centre of mass. Some factors that one would expect to enhance this work have been found to correlate with human sprinting performance: the fastest sprinters have a higher proportion of fast-twitch muscle fibres (Costill et al., 1976; Mero et al., 1981) and larger leg muscles (Abe et al., 2001; Kumagai et al., 2000). It is also reasonable to expect that the moment arm of a muscle would influence sprinting ability in complex ways. A muscle with a large moment arm about a joint has favourable mechanical advantage for generating torque about that joint, and large joint torques are needed to accelerate rapidly at the start of a race. Having a large moment arm, however, will also cause a muscle to shorten more for a given joint rotation (Carrier et al., 1994). Large moment arms should thus attenuate muscle force generation during shortening due to the force-velocity property (Nagano and Komura, 2003).

Classic research in comparative functional morphology suggests that the skeletal structure of the foot and ankle, in combination with muscle moment arms, are determinative of locomotor speed. The fastest running animals, such as cheetahs, have plantarflexor muscles that attach close to the ankle joint centre with a large distance between the point of application for the ground reaction force (GRF) and the joint centre (Hildebrand, 1960). Fast runners thus have higher 'gear ratios' (moment arm of the GRF divided by the moment arm of the muscle) than do walking, digging, or swimming animals (Carrier et

al., 1998; Hildebrand, 1960). It is also important to consider muscle moment arm in relation to muscle fascicle length. The ratio of the fascicle length to moment arm has been identified as a determinant of the range of joint motion over which a muscle may generate force (Alexander, 1981). This is a critical ratio because the muscle moment arm and the number of sarcomeres determine how much individual sarcomeres will shorten or lengthen for a given joint rotation.

There is evidence that the moment arms of the muscles important for locomotion have evolved for enhancing performance during dynamic rather than static tasks. The largest ankle moments produced statically by the frog gastrocnemius occur at joint angles for which neither muscle moment arm nor static muscle force is maximized (Lieber and Boakes, 1988). The musculoskeletal structure of frog limbs does, however, seem to maximize power generation during jumping. Muscle architecture, muscle moment arms, and movement dynamics combine to maximize the power generated by the semimembranosus muscle during a jump (Lutz and Rome, 1994). A similar tuning of musculoskeletal properties for dynamic tasks has not been documented in humans. It is unknown, for example, whether better human sprinters have muscle moment arms that are favourable for sprinting.

Previous investigations of anatomical structure in elite sprinters have revealed differences between sprinters and non-sprinters as well as correlations between musculoskeletal morphometry and sprinting ability. Ultrasound imaging has shown that sprinters have gastrocnemius and vastus lateralis muscles of greater thickness and with longer fascicles than those of non-sprinters (Abe et al., 2001). Kumagai et al. and Abe et al. showed that fascicle lengths and pennation angles of the same muscles correlated positively with performance in sprinters (Abe et al., 2000; Kumagai et al., 2000).

Longer muscle fibres have more sarcomeres and thus for a given fibre shortening velocity, the individual sarcomere shortening velocities would be slower in a longer fibre. At a given fibre shortening velocity, each sarcomere in a longer fibre would operate closer to isometric and thus would be able to generate more force, owing to the force-velocity property. Furthermore, for a given intrinsic sarcomere maximum shortening velocity, a longer fibre has a greater fibre maximum velocity (v_{\max}) because the sarcomere shortening velocities are additive (Bodine et al., 1982; Burkholder et al., 1994; Kumagai et al., 2000; Sacks and Roy, 1982). Alexander suggested that muscles with long fibres were suited for performing work during acceleration in dogs (Alexander, 1974). Pennation angle has been shown to have a weak correlation with force or speed production, and mainly influences the manner in which the fibres are packed within muscle to maximize force output (Burkholder et al., 1994). Although longer fibres and greater pennation would be expected to increase force for a given muscle shortening velocity, if tendon deformation is ignored, variation in muscle moment arm determines the change in muscle fibre length for a given joint rotation. Muscle moment arm thus has the potential to modulate the force production that would be useful to an accelerating sprinter. If a muscle with longer fibres has a proportionally greater moment arm, then the shortening velocity of the sarcomeres will be unaffected by the difference in fibre length. Conversely, short muscle moment arms may accentuate the benefits of long muscle fibres during a concentric contraction by reducing sarcomere shortening velocities.

There have been no studies of the muscle moment arms of sprinters, but there have been investigations of the Achilles' tendon moment arms of distance runners. Rosager et al. estimated moment arms from magnetic resonance imaging (MRI) and found no significant difference in moment arm between runners and non-runners (Rosager et al., 2002). Scholz et al., however, recently reported a strong correlation between moment arm and energetic cost during running in a study in which moment arms were determined by measuring the distance between the ankle and the tendon externally (Scholz et al., 2008). The authors used a mathematical model to explain how short moment arms should lead to increased storage of elastic energy in the Achilles' tendon and thus reduce metabolic energy consumption, although a link was not established between heel length and running performance.

The purpose of the present study was to measure the plantarflexion moment arms of the Achilles' tendon, plantarflexor muscle architecture parameters, and foot and ankle anthropometric characteristics in sprinters and non-sprinters. As in previous studies, the fascicle length and pennation angle of the gastrocnemius muscle were determined from ultrasound images but we were able to

examine these results along with moment arms measured in the same subjects. A simple mathematical model was used to simulate a sprinter's push-off during the first steps of a race in order to quantify the contribution of plantarflexor moment arm and foot structure to propulsive impulse.

MATERIALS AND METHODS

Participants

Twelve collegiate sprinters and 12 height-matched non-athletes not engaged in competitive sports participated in the study (Table 1). Seven of the sprinters were specialists in the 100 m (or long jumpers who trained with sprinters) who had self-reported personal best times ranging from 10.7 to 12.3 s, and the other five had 200 m times between 23.3 and 24.0 s. Participants gave informed consent and all procedures were approved by the Institutional Review Board of The Pennsylvania State University.

Ultrasonography

Ultrasonography was used to collect images of the lateral gastrocnemius and Achilles' tendon from which musculoskeletal structural properties were estimated. To determine muscle fascicle lengths and pennation angles, B-mode ultrasonography (Aloka 1100; transducer: SSD-625, 7.5 MHz and 39 mm scan width; Wallingford, CT, USA) was used to capture images from the central region of the right lateral gastrocnemius muscle (Fig. 1) while each participant stood quietly in anatomical position with the probe aligned along the muscle belly. The lateral gastrocnemius muscle was chosen primarily because it is superficial but also because it has the longest fascicle lengths of any of the triceps surae, thus giving it greater potential to generate force during explosive movements requiring higher shortening velocity (Kumagai et al., 2000). Ultrasound aqueous gel was applied to the skin to enhance propagation of the ultrasonic waves. Ultrasound images were enhanced and digitized using routines custom-written in MATLAB (Mathworks, Inc; Natick, MA, USA). The pennation angle was measured as the angle between the fascicular path and the deep aponeurosis (Abe et al., 2001; Abe et al., 2000; Kumagai et al., 2000). Fascicle length l_f was estimated using the muscle thickness t , the distance between the superficial and deep aponeuroses, and the pennation angle θ according to $l_f = t/\sin\theta$ (Abe et al., 2001; Abe et al., 2000; Kumagai et al., 2000). Measurements were repeated on a second day for three non-sprinter subjects to assess reliability; average differences in fascicle length and pennation angle were 1.2 mm and 0.5 deg., respectively.

Ultrasound imaging was also used to determine tendon excursion during ankle plantarflexion in order to compute the plantarflexion

Table 1. Anthropometric characteristics and ages of the sprinter and non-sprinter subjects

	Sprinters	Non-sprinters	<i>P</i> -value
Stature (cm)	181.4±8.0	180.9±7.6	0.874
Body mass (kg)	77.0±6.5	76.8±9.5	0.954
Age (years)	19.3±1.2	25.4±2.8	<0.001
Fibular head to lateral malleolus (cm)	41.1±2.6	44.1±3.5	0.026
Heel to toe (cm)	27.4±1.1	26.9±2.0	0.473
Heel to 1st metatarsal head (cm)	19.2±0.9	19.5±1.6	0.485
Heel to lateral malleolus (cm)	5.5±0.7	5.6±0.3	0.594
Lateral malleolus to 1st metatarsal head* (cm)	13.7±0.7	13.9±1.4	0.589
Lateral malleolus to toe* (cm)	21.9±0.9	21.3±1.8	0.305
First metatarsal head to toe* (cm)	8.2±1.0	7.3±0.9	0.032

Values are means ± 1 s.d. *P*-values are for two-tailed *t*-tests for mean differences between groups.

*These quantities were not measured directly, but were derived by subtraction from measured quantities.

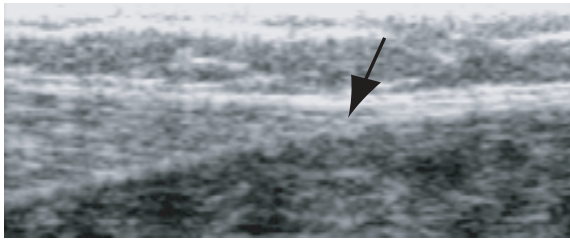


Fig. 1. Ultrasound image of the lateral gastrocnemius. The arrow indicates the musculotendinous junction, the landmark used for tracking excursion of the Achilles' tendon during applied ankle rotation.

moment arm of the Achilles' tendon. Each participant sat with the right knee fully extended and the thigh held in place with respect to the base of the test apparatus (Fig. 2). The right foot was secured with Velcro® straps to a foot platform that was hinged so that it rotated in the sagittal plane. The hinge axis was directed mediolaterally and was approximately aligned with the malleoli, and a potentiometer (Midori Precisions, CP-2FK, Tokyo, Japan; repeatability $\pm 0.005\%$, linearity $\pm 1\%$) attached to the foot platform was used to record the ankle joint rotation. Potentiometer voltages were linear with platform rotation (calibration coefficient = 68.9 deg./1 V ; $R^2 = 0.9991$) and were recorded using a data acquisition system consisting of a National Instruments analogue to digital (A/D) converter (Dataq Instruments, DI, 148U, OH, USA) and a personal computer. The A/D converter had a measurement range of $\pm 10 \text{ V}$ and resolution of $\pm 19.5 \text{ mV}$ and a maximum sample rate of 240 Hz . The data acquisition software (Windaq/Lite, Dataq Instruments, OH, USA) averaged the signal such that the output had a resolution of $\pm 2 \text{ mV}$.

During a trial, one experimenter manually rotated the foot from approximately 10 deg. dorsiflexion to 20 deg. plantarflexion in 3 s while a second experimenter held the ultrasound probe against the skin longitudinally on the posterior distal third of the leg at the appropriate musculotendinous junction, where the gastrocnemius muscle inserts into the Achilles' tendon. Ultrasound images captured at 30 Hz during each trial were digitized and saved to a personal computer with a frame grabber card (Scion Corporation, LG-3, Frederick, MD, USA) with the imaging software, Scion Imaging

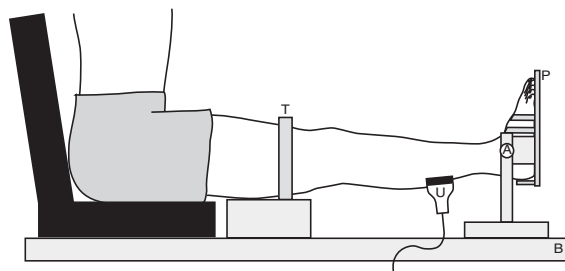


Fig. 2. Schematic diagram of the apparatus used to apply foot rotations. The subject's right foot was strapped to a platform (P) that was rotated manually from dorsiflexion to plantarflexion about a mediolateral axis (A) with respect to the base of the apparatus (B) by one experimenter while sagittal plane rotation was recorded using a potentiometer and a second experimenter held an ultrasound probe (U) against the shank. The ultrasound probe was fitted into a custom-made foam pad that reduced slipping of the probe along the skin. The thigh was held in place relative to the base by a padded aluminium arch (T).

(Scion Corporation). Participants were instructed to plantarflex maximally during these trials to minimize artefacts resulting from variation in tendon tension during the movement (Maganaris et al., 1998a). Tendon excursion was measured as the displacement of the musculotendinous junction computed from the ultrasound images using an automated algorithm for tracking image features between frames (Lee et al., 2008). Five foot rotation trials were performed for each participant.

The plantarflexion moment arm of the Achilles' tendon was calculated as the first derivative of tendon excursion *versus* joint angle (An et al., 1984). Achilles' tendon excursions were generally linear with respect to ankle angle, and the slopes of lines fitted to these data were taken to represent the moment arm for each trial. Each participant's moment arm was found by averaging the five foot rotation trials. Measurements were repeated on a second day for three non-sprinter subjects to assess reliability; the average difference in moment arm was 3.2 mm .

Anthropometry

Distances between various bony landmarks on the right lower legs of all subjects were made using a millimetre-graded tape measure. Subjects stood in anatomical position while the experimenter measured, (1) the distances between the head of the fibula and the lateral malleolus, (2) the anteroposterior (AP) distance from the most posterior point on the heel to the most anterior point on the toes, (3) the AP distance from the heel to the first metatarsal head, and (4) the AP distance from the heel to the lateral malleolus. Additional measurements of distances between landmarks on the foot were derived *post-hoc* by subtracting these measurements from one another.

Statistics

Two-tailed *t*-tests were used to test for differences ($\alpha = 0.05$) between sprinters and non-sprinters in lateral gastrocnemius thickness, lateral gastrocnemius pennation angle, lateral gastrocnemius fascicle length, Achilles' tendon moment arm, the ratio of fascicle length to moment arm, and the various anthropometric measures.

Computer model

To study how sprint performance is affected by muscle and joint structure in the context of the movement dynamics, a planar, forward-dynamic computer simulation of a sprinter's push-off was developed (Fig. 3). The mass m of the sprinter (75 kg) was concentrated at a point 1 m above the ankle connecting the 'body' segment to the 'foot' segment. The foot was a massless link with 14 cm between the ankle and metatarsophalangeal (MTP) joint, where another revolute connected the foot to a third massless 'toe' link, 7.5 cm long. The distal end of the toe link was connected to ground by a third revolute joint, and the proximal end of the toe was supported by a damped spring ($k = 2.0 \times 10^5 \text{ N m}^{-1}$; $b = 250 \text{ N s m}^{-1}$; k is stiffness and b is the damping coefficient) that resisted penetration of this point into the floor. Torsional springs with stiffness of 100 Nm rad^{-1} resisted ankle plantar flexion beyond 60 deg. and toe extension beyond 60 deg. Two Hill-type muscle-tendon actuators (Hill, 1938) represented the collective triceps surae and toe flexor muscle groups. The maximum isometric force for the plantarflexor and toe flexor actuators were set at 6660 N and 948 N , respectively. These values were obtained by summing the values for each group as represented in the lower extremity model of Delp et al. (Delp et al., 1990) and then multiplying by 1.5 to reproduce the hypertrophy that would be expected in a sprinter. The plantarflexor actuator originated 40 cm proximal to the ankle on the

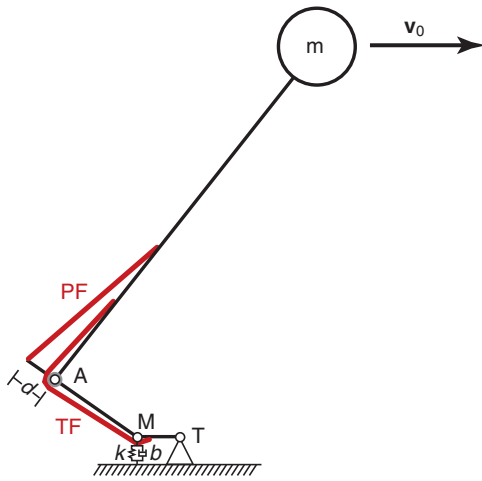


Fig. 3. Planar three-segment, three-degree-of-freedom computational model used to simulate a sprinter's push-off. The simulation began with the point mass, m , translating forward with velocity $v_0=2\text{ m s}^{-1}$ and ended when contact was broken at the toe (T). The proximal end of the toe segment was supported at the metatarsophalangeal joint (M) by a damped spring with stiffness k and the damping coefficient b . Excitation controls for plantarflexor (PF) and toe flexor (TF) actuators were determined using parameter optimization. The plantarflexion moment arm of the PF actuator was approximated by the distance d between the ankle A and the actuator's insertion on the foot segment.

body segment and inserted posterior to the ankle on the foot segment (see below), whereas the toe flexor originated 20 cm proximal to the ankle, wrapped around cylindrical surfaces with radii of 15 mm and 6 mm at the ankle and MTP joints, and inserted 10 mm distal to the MTP joint on the toe segment. Pennation angles for both muscle-tendon actuators were set at 0 deg. across simulations. Optimal fibre length l_0 was 4 cm for each muscle-tendon actuator and tendon slack length was chosen such that optimal fibre lengths were attained in 30 deg. plantarflexion, a choice guided by the sarcomere lengths recently reported for the triceps surae and toe flexors by Ward et al. (Ward et al., 2009). Actuator tendons were compliant, with normalized force-length curves defined according to Zajac (Zajac, 1989). Muscle force was computed using a Hill-type model developed by Schutte (Schutte, 1992). The force-length and shortening force-velocity relations used were those specified by Hatze (Hatze, 1977) and Hill (Hill, 1938). The maximum shortening velocity v_{\max} for each muscle actuator was set at $10l_0\text{ s}^{-1}$ (Zajac, 1989). The equations of motion for the system were developed and integrated using SIMM with Dynamics Pipeline (Musculographics, Inc.; Santa Rosa, CA, USA) and SD/FAST (Parametric Technology Corp.; Needham, MA, USA).

Excitation controls for the muscle-tendon actuators were determined by solving a parameter optimization problem in which

the 43 parameters were the final time t_f and 21 excitation nodes for each actuator evenly spaced in time between $t=0$ and $t=t_f$. Excitations for each actuator, $u_{\text{toe flexor}}(t)$ and $u_{\text{plantarflexor}}(t)$, were determined by linear interpolation between nodes. An objective function J was defined according to:

$$J(u_{\text{toe flexor}}(t), u_{\text{plantarflexor}}(t), t_f) = 1000 \times (F_V(t_f) / mg)^2 - (v_x(t_f)/v_0) - (y_0 - y(t_f)) / L, \quad (1)$$

such that minimizing J accomplished the following: (1) ensured that the final vertical reaction force at the toe, $F_V(t_f)$ normalized by the model weight was very close to zero; (2) maximized the horizontal velocity v_x of the mass at t_f normalized by the initial horizontal velocity v_0 ; and (3) minimized the vertical drop of the mass occurring between $t=0$ and $t=t_f$ normalized by the length of the body link, L , where $y(t_f)$ is the height of the mass at the final time and y_0 is its initial height. The last of these terms was necessary to prevent the model from maximizing forward velocity at toe-off by 'diving' forward. Minimization of J was accomplished using a hybrid particle swarm optimization and downhill simplex method that was found to converge reliably from varied initial guesses for the parameter values.

One set of simulations of sprint push-off were conducted with d , the posterior distance from the ankle to insertion of the tendon, varying between 25 mm and 50 mm in 5 mm increments while toe length was held at 75 mm. The distance d differed from the perpendicular distance from the ankle to the plantarflexor muscle in neutral position by less than 1% and so was taken to be a reasonable approximation of the plantarflexor moment arm in that position (although d differed from moment arm at high plantarflexion angles). A second set of simulations was conducted with d fixed at 35 mm while the length of the toe link was varied from 65 mm to 90 mm in 5 mm increments. Each simulation began with the ankle in 10 deg. dorsiflexion, the toes extended by 35 deg., and the point mass travelling to the right at $v_0=2\text{ m s}^{-1}$. For each simulation, the horizontal impulse was computed as the change in the horizontal momentum occurring over the course of the simulation. Horizontal impulse was selected as the output of interest because it represents the increase in forward velocity and the forward impulse delivered during individual steps in the acceleration phase of the sprint has been shown to correlate with overall sprint performance (Hunter et al., 2005).

RESULTS

The plantarflexion moment arms of the sprinters were 25% smaller than those of non-sprinters (Table 2) and this difference was highly significant ($P<0.001$). Sprinters also had significantly ($P=0.024$) longer fascicles than those of non-sprinters. Consequently, the mean ratio of fascicle length to plantarflexor lever arm was nearly 50% higher in sprinters than in non-sprinters ($P<0.001$). No significant difference was found between the pennation angles of sprinters and those of non-sprinters ($P=0.212$).

Table 2. Musculoskeletal architecture parameters for the lateral gastrocnemius measured from ultrasound images

	Sprinters	Non-sprinters	P-value
LG thickness (mm)	15.5±1.9	14.7±2.0	0.330
LG pennation angle (deg.)	12.8±1.2	13.7±2.1	0.212
LG fascicle length (mm)	69.9±6.2	62.7±8.3	0.024
Achilles' tendon moment arm (mm)	31.0±3.7	41.6±5.5	<0.001
Fascicle length:moment arm	2.28±0.32	1.53±0.27	<0.001

LG, lateral gastrocnemius.

Values are means ± s.d. P-values are for two-tailed t-tests for mean differences between groups.

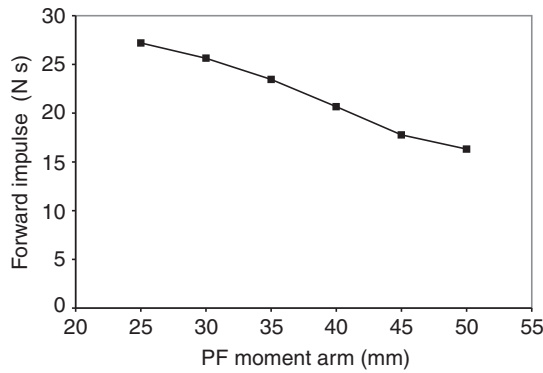


Fig. 4. Forward impulse imparted to the mass during the push-off simulations for which the plantarflexor moment arm was varied and toe length was held constant at 75 mm. Forward impulse was greatest when the moment arm was shortest.

The sprinters and non-sprinters were height-matched, resulting in no significant difference in height ($P=0.874$) between the groups, but two of the anthropometric measures were found to differ between groups (Table 1). The mean toe length (AP distance from the first metatarsal head to the tip of the toes) of the sprinters was 9 mm longer than that of the non-sprinters ($P=0.032$). The length of the shank (fibular head to lateral malleolus) was 30 mm shorter in sprinters ($P=0.026$). All other differences in anthropometric measures were found to be non-significant (all $P \geq 0.305$).

The propulsive impulse imparted to the model in the computer simulations was found to depend on both plantarflexor muscle moment arm (Fig. 4) and toe length (Fig. 5). As plantarflexion moment arm was decreased from 50 mm to 25 mm, forward impulse increased by 10.9 Ns (40%). As toe length was increased from 65 mm to 90 mm, forward impulse increased by 3.1 Ns (14%).

The increases in simulated forward impulses that resulted from decreases in plantarflexor moment arm were accompanied by generally longer plantarflexor fibre lengths and slower plantarflexor shortening velocities (Fig. 6). At toe-off, the plantarflexor fibre length, was 0.72 (normalized by l_0) when the plantarflexor moment arm was 25 mm, but only 0.43 l_0 when the moment arm was 50 mm. Peak plantarflexor shortening velocity was 0.46 v_{\max} when the plantarflexor moment arm was 25 mm and 0.80 v_{\max} when the moment arm was 50 mm. Lengthening of the toes produced fibre

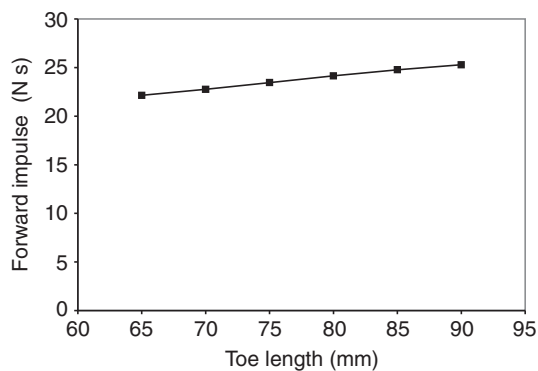


Fig. 5. Forward impulse imparted to the mass during the push-off simulations for which toe length was varied and toe length was held constant at 35 mm. Forward impulse was greatest when the toes were longest.

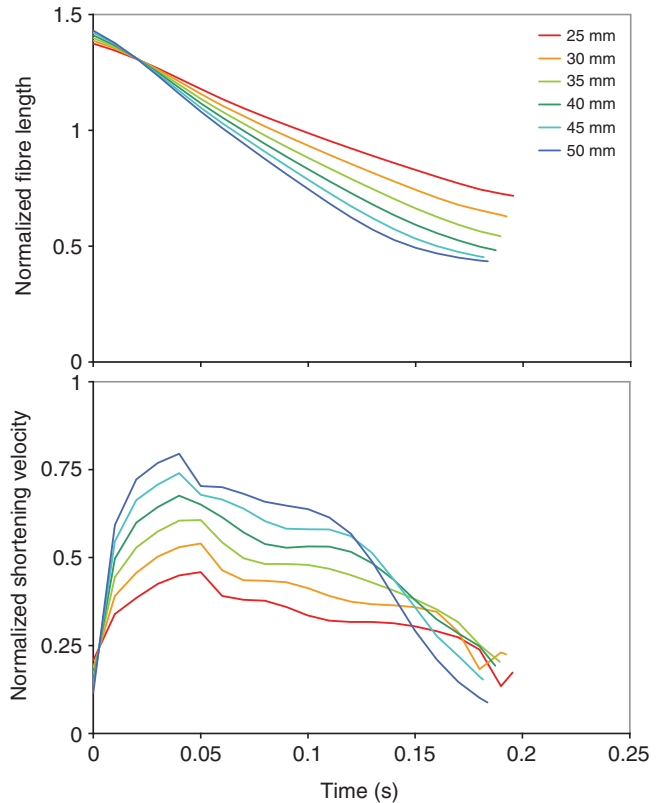


Fig. 6. Plantarflexor muscle fibre behaviour during the push-off simulations for which the plantarflexor moment arm was varied and toe length was held constant at 75 mm. Muscle fibre length (normalized by l_0) was maintained best (top) and peak fibre shortening velocity (normalized by v_{\max}) was least (bottom) for simulations in which the moment arm was shortest.

length and velocity changes that were similar to those produced by shortening the plantarflexor moment arm, but to a much lesser degree (Fig. 7). Increases in forward impulse occurring with longer toes were also attributable to longer contact times, which were 13% greater for the 90 mm toes as compared with the 65 mm toes. Contact time was only 6% greater for the 25 mm plantarflexor moment arm than for the 50 mm moment arm.

DISCUSSION

The goal of this study was to determine if the foot and ankle structure of sprinters differs from that of non-sprinters in a manner that contributes positively to forward acceleration, and thus sprint performance. Although maximal sprinting is likely to be aided by substantial plantarflexion moments, it does not appear that the generation of such moments is aided by abnormally large plantarflexor muscle moment arms. Instead, we found that these plantarflexor moment arms are 25% smaller in sprinters than in non-sprinters. We also found that sprinters have longer gastrocnemius fascicles, a finding that agrees with the results of previous studies (Abe et al., 2001; Abe et al., 2000; Kumagai et al., 2000). The longer fascicles and shorter moment arms of the sprinters combined to produce ratios of gastrocnemius fascicle length to plantarflexion moment arm that were substantially higher for sprinters. In addition, sprinters were found to have longer toes and shorter lower legs than those of non-sprinters, anthropometric differences that have not been reported previously.

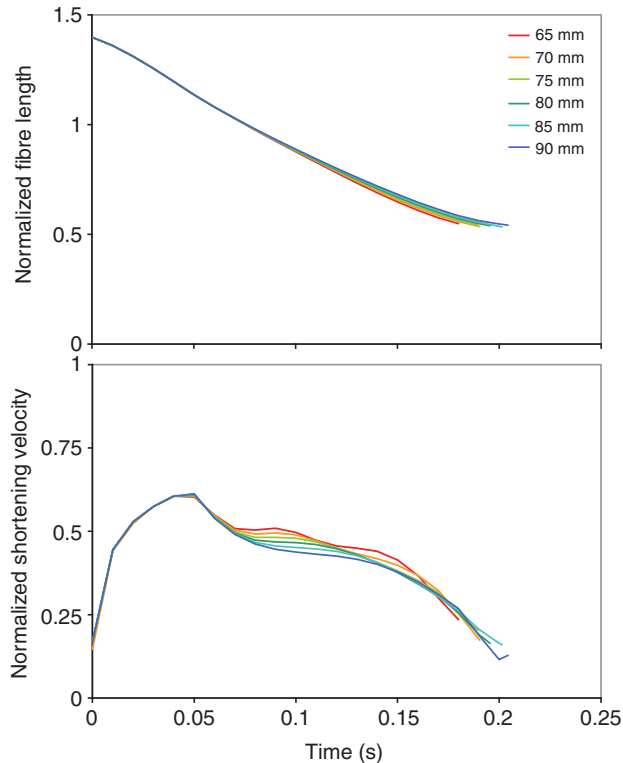


Fig. 7. Plantarflexor muscle fibre behaviour during the push-off simulations for which toe length was varied and toe length was held constant at 35 mm. Muscle fibre length (top; normalized by l_0) was slightly greater and peak fibre shortening velocity (bottom; normalized by v_{max}) was slightly less for simulations in which toes were longest.

The plantarflexor moment arms of the non-sprinter subjects of the present study are about 1 cm shorter than those reported previously by authors who measured moment arms *in vivo* using MRI [magnetic resonance imaging (Maganaris et al., 1998a; Rosager et al., 2002; Rugg et al., 1990)]. This difference between Achilles' tendon moment arms computed from ultrasound images of tendon excursion and moment arms obtained from MRI scans has been documented previously by Maganaris et al. (Maganaris et al., 2000). The authors of that study attributed the disagreement between the two methods to differences in the fundamental assumptions of each method: when using MRI it is assumed that the centre of rotation between the calcaneus and talus is accurately located using the Reuleaux method, whereas the use of ultrasound assumes that tendon excursion may be measured accurately. While acknowledging that there is no 'gold standard' for moment arm measurement, the authors did advocate that a scaling factor of 1.22–1.27 be applied to Achilles' tendon moment arms measured using ultrasound to obtain corresponding moment arms measured using MRI. If we scale the mean value obtained for our non-sprinter subjects (41.6 mm), for the sake of comparison, we obtain a scaled moment arm of 51.8 mm, a value that is highly consistent with previously-reported MRI-based measurements.

The results of this study have implications for the manner in which sprint performance depends upon muscle structure as well as composition. While maximum muscle shortening velocity may be attributed in part to biochemical properties (Bodine et al., 1982; Sacks and Roy, 1982; Spector et al., 1980), muscle architecture may be a determinant that is at least as important (Burkholder et al.,

1994; Sacks and Roy, 1982). In the present study, it was found that the muscle fascicles of the lateral gastrocnemius are longer in sprinters than in non-sprinters a finding previously made by Abe et al. (Abe et al., 2001; Abe et al., 2000). Longer fascicles may improve sprint performance; gastrocnemius fascicle length (Abe et al., 2001) is negatively correlated with 100 m race times in elite sprinters (Abe et al., 2000). The lateral gastrocnemius pennation angles found for sprinter and non-sprinter subjects in the present study are similar to the values measured by Abe et al. but significant differences in pennation between these groups were not found in that study or in ours (Abe et al., 2000).

Although we did not measure optimal fibre lengths, the moment arms and fascicle lengths we found suggest that sprinters achieve rapid acceleration using relatively short plantarflexor moment arms that do not scale with muscle fibre length. The short moment arms reduce the mechanical advantage of the plantarflexors, but in combination with long fibre lengths they should also enhance muscle force generation during contractions performed at high shortening velocities. Computer simulations of isokinetic plantarflexion exercises have suggested that Achilles' tendon moment arms at the smaller end of the range typically seen in humans produce higher joint moments and increased power output (Nagano and Komura, 2003). It has also been suggested that there is a relationship between the mechanical advantage of a muscle and its proportion of type II muscle fibres (Gandevia and Mahutte, 1980) since muscles with small moment arms must develop large forces, and fast motor units can develop more tension than slower ones (Garnett et al., 1978).

To our knowledge, the present study is the first investigation of plantarflexor moment arms in sprinters, although such measurements have been made in distance runners. Achilles' tendon moment arm has recently been shown to inversely correlate with the cost of locomotion in distance runners, perhaps because short moment arms require greater muscle force and thus promote elastic energy storage in tendons (Scholz et al., 2008). Aramptazis et al. did not directly report gastrocnemius moment arms of distance runners of varying abilities, but did state that no differences existed in the ratios of tendon and aponeurosis elongation to joint rotation, which is equivalent to moment arm (Aramptazis et al., 2006). Rosager et al. reported no differences between the Achilles' tendon moment arms of high-mileage distance runners and non-runners (Rosager et al., 2002).

Longer toes may enhance forward acceleration through multiple mechanisms. Carrier et al. suggested that the increase in the 'gear ratio' of the lever arm of the GRF to the lever arm of the Achilles' tendon that occurs as the centre of pressure progresses anteriorly during stance would produce higher plantarflexor forces because of favourable force–velocity behaviour (Carrier et al., 1994). The simulation results of the present study show that longer toes, which also effectively increase the gear ratio, may have such an effect on plantarflexor force. Longer toes also were found to increase contact time in the simulations, which would permit more time for acceleration of the centre of mass during the first phase of a sprint race. A recent study by Rolian et al. showed that the work done by the toe flexors of distance runners correlated with toe length, suggesting that short toes are more energetically economical and thus favourable for distance running (Rolian et al., 2009). Noting that the toes of primitive hominins were longer than those of modern humans, the authors proposed that short toes have been selected for because of evolutionary pressure for efficient distance running. In our simulations longer toes did result in more muscle work being done, but most of this was attributable to the plantarflexors. Although avoiding additional muscle work might be viewed as

inefficient for a distance runner travelling at a constant velocity, it appears to be useful to an accelerating sprinter. The fact that the toes of modern humans are considerably shorter than our ape relatives and fossil ancestors suggests that the need for endurance and economy may have outweighed the need for rapid accelerations in our ancestors.

A small Achilles' tendon moment arm may enhance sprint performance by enhancing muscle force generation, but this determination should be made with reference to the movement dynamics of the task. The rate of ankle joint rotation partially determines plantarflexor force through force-velocity effects, but the rate of joint rotation will itself be determined in part by plantarflexor moments. Although the sprint start does require large plantarflexor power generation (Johnson and Buckley, 2001) and the positive work done by the plantarflexors has been shown to be highly correlated with stride length and stride frequency (Ae et al., 1985), it appears that this is achieved by sacrificing mechanical advantage in favour of an arrangement that reduces sarcomere shortening velocity and better maintains sarcomere length during rapid plantarflexion. Longer toes raise the gear ratio (Carrier et al., 1994) by increasing the numerator (lever arm of the GRF), but a smaller plantarflexor moment arm will have the same effect, by decreasing the denominator. Investigations of muscle moment arms in fast-running animals such as the racing greyhound (Williams et al., 2008) revealed that the latissimus dorsi, which has a propulsive role during sprinting, has a high muscle fibre length to moment arm ratio similar to the high fascicle length to moment arm ratios we observed in sprinters. The authors suggested that this high ratio allows generation of large torques over a wide range of motion at fast joint angular velocities. Smith et al. suggested that the role played by small moment arms of the ankle muscles of ostriches in increasing joint angular velocity may be more important than increasing moment with a large moment arm during sprinting (Smith et al., 2007). Effective mechanical advantage, the ratio of the extensor muscle moment arm to the moment arm of the GRF, has been found to not be influenced by increasing running speed, across cursorial animals (Biewener, 1989). However, the effective mechanical advantage did scale with increased body mass across species, which may explain the ability of animals to reduce the mass-specific force of the muscles as body mass increases. Muscle-powered accelerations such as those in frog jumping can also be influenced by the effective mechanical advantage (Roberts and Marsh, 2003). Roberts and Marsh demonstrated that frogs have poor mechanical advantage early in jumping that improves during the movement. This enhances the elastic storage and release of energy, which improves jumping performance, similar to the mechanism of increased elastic energy storage following from short plantarflexor moment arms in distance runners proposed by Scholz et al. (Scholz et al., 2008).

It is unknown to what degree the differences in muscle and joint architecture between the sprinter and non-sprinter subjects may be attributed to sprint training. The longer muscle fascicles found in sprinter subjects are likely to represent a normal adaptive response similar to that demonstrated in animal models in which sarcomere number increases as a result of training (Ashmore and Summers, 1981; Lynn et al., 1998; Williams and Goldspink, 1978). In humans, differences in muscular architecture as a result of training have been observed by Kearns et al. who reported larger leg muscles and longer fascicle length in the dominant legs of junior soccer players (Kearns et al., 2001). Abe found no differences between the lateral gastrocnemius fascicle lengths of athletes and their monozygous non-athlete twins (Abe, 2002), but did observe differences in medial gastrocnemius fascicle length. Although there is evidence

for fascicle lengths changing in response to training, adaptations that alter moment arms would require modification of bony geometry or tendon insertion migration that has not been established as yet. Such responses to endurance running have been investigated but not observed to occur in sheep (Zumwalt, 2006). If sprinters' short moment arms are attributable to immutable skeletal characteristics, this would support the coaches' adage that, 'The sprinter is born not made' (Bannister, 1994).

Certain limitations were associated with the data collection in the present study. The rotation axis of the apparatus we used was aligned with the mediolateral axis and located such that it passed approximately through the malleoli. Although this approach is consistent with the practices of previous investigators who made measurements of plantarflexor moment arms (Maganaris et al., 1998b; Rosager et al., 2002), it is important to acknowledge the multiplanar nature of natural ankle complex rotations. Different moment arms might have been measured if supination-pronation (i.e. a combination of plantarflexion-dorsiflexion and inversion-eversion) had been imposed or if ankle angle had been quantified differently. It is also important to note that the fascicle lengths we measured may not be indicative of muscle fibre lengths as fibres may not span the entire length of a fascicle (Hijikata and Ishikawa, 1997), fascicle paths may not be well approximated by straight lines in the plane of the ultrasound image, and fibre thickness effects were not accounted for. In addition, we measured architectural parameters for only one of the triceps surae, the lateral gastrocnemius. Because we did not count sarcomeres, we cannot draw conclusions about the optimal fibre lengths of the subjects in this study. In addition, it has been shown that a more elastic tendon allows muscle fibres to shorten more slowly, yielding higher force generation (Bobbert, 2001; Hof, 1998; Roberts, 2002) and perhaps influencing measurements of tendon excursion. However, Kubo et al. reported that the compliance of the tendon of the medial gastrocnemius at high force was similar between sprinters and non-sprinters (Kubo et al., 2000). It is also important to note that sprinting ability depends upon many factors not considered in our experimental study or varied in our simulation, including training methods and muscle composition.

The three-degree-of-freedom simulation of sprint push-off employed the simplest possible model that would be useful for investigating the effects of varied plantarflexor moment arm and toe length. Its planar nature and lack of hip and knee joints made it ill-suited for examination of the effects of foot rotation and the potential benefits of the shorter lower legs that we measured in sprinters. A more complex model of the foot-ground interaction and fewer assumptions regarding the force-generating capacities of the muscle-tendon actuators would also be desirable. Sensitivity studies were performed to determine the influence of plantarflexor tendon compliance, forefoot length (ankle to MTP), ankle angle at which optimal fibre length was attained, and initial forward velocity v_0 . Neither changing the slope of the linear portion of the tendon force-length curve by 50%, forefoot length by 2 cm, nor the critical ankle angle by 20 deg. altered the general character of the relationships shown in Figs 4 and 5. Doubling the initial forward velocity to 4.0 m s^{-1} , however, greatly reduced forward impulse magnitude and the influences of both plantarflexor moment arm and toe length on forward impulse. These differences occurred because of decreased contact time and increased plantarflexion velocity. Muscle forces were thus reduced and also had less time to influence forward acceleration.

The experimental and computational modelling results of the present study provide insight into the determinants of muscle

function during sprinting. In addition, the results illustrate the importance of considering joint structure as well as muscle architecture in determining the functional roles of muscles during movements in which muscle rapidly shortens. Assessment of muscle function during activities in which muscle rapidly shortens should consider muscle moment arm, not only as an indicator of mechanical advantage, but also as a determinant of muscle force generation.

We thank Mr Emre Ak for assistance with the data collection and Dr Campbell Rolian for a valuable comment we have incorporated into the Discussion. This work was supported by the National Science Foundation (BCS-0134217).

REFERENCES

- Abe, T. (2002). Fascicle length of gastrocnemius muscles in monozygous twins. *J. Physiol. Anthropol. Appl. Human Sci.* **21**, 291-295.
- Abe, T., Kumagai, K. and Brechue, W. F. (2000). Fascicle length of leg muscles is greater in sprinters than distance runners. *Med. Sci. Sports Exerc.* **32**, 1125-1129.
- Abe, T., Fukashiro, S., Harada, Y. and Kawamoto, K. (2001). Relationship between sprint performance and muscle fascicle length in female sprinters. *J. Physiol. Anthropol. Appl. Human Sci.* **20**, 141-147.
- Ae, M., Miyashita, K., Shibukawa, K., Yokoi, T. and Hashihara, Y. (1985). Body segment contributions during the support phase while running at different velocities. In *Biomechanics IX-B* (ed. D. A. Winter, R. W. Norman, R. P. Wells, K. C. Hayes and A. E. Patla), pp. 343-349. Champaign, IL: Human Kinetics.
- Alexander, R. M. (1974). The mechanics of jumping by a dog (*Canis familiaris*). *J. Zool.* **173**, 549-573.
- Alexander, R. M. (1981). Allometry of the leg muscles of mammals. *J. Zool.* **194**, 539-552.
- An, K. N., Takahashi, K., Harrigan, T. P. and Chao, E. Y. (1984). Determination of muscle orientations and moment arms. *J. Biomech. Eng.* **106**, 280-282.
- Arampatzis, A., De Monte, G., Karamanidis, K., Morey-Klapsing, G., Stafilidis, S. and Bruggemann, G. P. (2006). Influence of the muscle-tendon unit's mechanical and morphological properties on running economy. *J. Exp. Biol.* **209**, 3345-3357.
- Ashmore, C. R. and Summers, P. J. (1981). Stretch-induced growth in chicken wing muscles: myofibrillar proliferation. *Am. J. Physiol.* **241**, C93-C97.
- Bannister, R. (1994). *The Four-Minute Mile*. Guilford, CT: The Lyons Press.
- Baumann, W. (1976). Kinematic and dynamic characteristics of the sprint start. In *Biomechanics V-B* (ed. P. V. Komi). Baltimore: University Park Press.
- Biewener, A. A. (1989). Scaling body support in mammals: limb posture and muscle mechanics. *Science* **245**, 45-48.
- Bobbert, M. F. (2001). Dependence of human squat jump performance on the series elastic compliance of the triceps surae: a simulation study. *J. Exp. Biol.* **204**, 533-542.
- Bodine, S. C., Roy, R. R., Meadows, D. A., Zernicke, R. F., Sacks, R. D., Fournier, M. and Edgerton, V. R. (1982). Architectural, histochemical, and contractile characteristics of a unique biarticular muscle: the cat semitendinosus. *J. Neurophysiol.* **48**, 192-201.
- Burkholder, T. J., Fingado, B., Baron, S. and Lieber, R. L. (1994). Relationship between muscle fiber types and sizes and muscle architectural properties in the mouse hindlimb. *J. Morphol.* **221**, 177-190.
- Carrier, D. R., Heglund, N. C. and Earls, K. D. (1994). Variable gearing during locomotion in the human musculoskeletal system. *Science* **265**, 651-653.
- Carrier, D. R., Gregersen, C. S. and Silvertown, N. A. (1998). Dynamic gearing in running dogs. *J. Exp. Biol.* **201**, 3185-3195.
- Costill, D. L., Daniels, J., Evans, W., Fink, W., Krahenbuhl, G. and Saltin, B. (1976). Skeletal muscle enzymes and fiber composition in male and female track athletes. *J. Appl. Physiol.* **40**, 149-154.
- Delp, S. L., Loan, J. P., Hoy, M. G., Zajac, F. E., Topp, E. L. and Rosen, J. M. (1990). An interactive graphics-based model of the lower extremity to study orthopaedic surgical procedures. *IEEE Trans. Biomed. Eng.* **37**, 757-767.
- Gandevia, S. C. and Mahutte, C. K. (1980). Joint mechanics as a determinant of motor unit organization in man. *Med. Hypotheses* **6**, 527-533.
- Garnett, R., O'Donovan, M. J., Stephens, J. A. and Taylor, A. (1978). Evidence for the existence of three motor unit types in normal human gastrocnemius. *J. Physiol.* **280**, 65P.
- Hatze, H. (1977). A myocybernetic control model of skeletal muscle. *Biol. Cybern.* **25**, 103-119.
- Hijikata, T. and Ishikawa, H. (1997). Functional morphology of serially linked skeletal muscle fibers. *Acta Anat. (Basel)* **159**, 99-107.
- Hildebrand, M. (1960). How animals run. *Sci. Am.* **202**, 148-157.
- Hill, A. V. (1938). The heat of shortening and the dynamic constants of muscle. *Proc. R. Soc. London Series A* **126**, 136-195.
- Hof, A. L. (1998). In vivo measurement of the series elasticity release curve of human triceps surae muscle. *J. Biomech.* **31**, 793-800.
- Hunter, J. P., Marshall, R. N. and McNair, P. J. (2005). Relationships between ground reaction force impulse and kinematics of sprint-running acceleration. *J. Appl. Biomech.* **21**, 31-43.
- Johnson, M. D. and Buckley, J. G. (2001). Muscle power patterns in the mid-acceleration phase of sprinting. *J. Sports Sci.* **19**, 263-272.
- Kearns, C. F., Isokawa, M. and Abe, T. (2001). Architectural characteristics of dominant leg muscles in junior soccer players. *Eur. J. Appl. Physiol.* **85**, 240-243.
- Kubo, K., Kanehisa, H., Takeshita, D., Kawakami, Y., Fukashiro, S. and Fukunaga, T. (2000). In vivo dynamics of human medial gastrocnemius muscle-tendon complex during stretch-shortening cycle exercise. *Acta Physiol. Scand.* **170**, 127-135.
- Kumagai, K., Abe, T., Brechue, W. F., Ryushi, T., Takano, S. and Mizuno, M. (2000). Sprint performance is related to muscle fascicle length in male 100-m sprinters. *J. Appl. Physiol.* **88**, 811-816.
- Lee, S. S., Lewis, G. S. and Piazza, S. J. (2008). An algorithm for automated analysis of ultrasound images to measure tendon excursion in vivo. *J. Appl. Biomech.* **24**, 75-82.
- Lieber, R. L. and Boakes, J. L. (1988). Muscle force and moment arm contributions to torque production in frog hindlimb. *Am. J. Physiol.* **254**, C769-C772.
- Lutz, G. J. and Rome, L. C. (1994). Built for jumping: the design of the frog muscular system. *Science* **263**, 370-372.
- Lynn, R., Talbot, J. A. and Morgan, D. L. (1998). Differences in rat skeletal muscles after incline and decline running. *J. Appl. Physiol.* **85**, 98-104.
- Maganaris, C. N., Baltzopoulos, V. and Sargeant, A. J. (1998a). Changes in Achilles tendon moment arm from rest to maximum isometric plantarflexion: in vivo observations in man. *J. Physiol.* **510**, 977-985.
- Maganaris, C. N., Baltzopoulos, V. and Sargeant, A. J. (1998b). In vivo measurements of the triceps surae complex architecture in man: implications for muscle function. *J. Physiol.* **512**, 603-614.
- Maganaris, C. N., Baltzopoulos, V. and Sargeant, A. J. (2000). In vivo measurement-based estimations of the human Achilles tendon moment arm. *Eur. J. Appl. Physiol.* **83**, 363-369.
- Mero, A., Luhtanen, P. and Viitasalo, J. T. (1981). Relationships between the maximal running velocity, muscle fiber characteristics, force production and force relaxation of sprinters. *Scand. J. Sports Sci.* **3**, 16-22.
- Nagano, A. and Komura, T. (2003). Longer moment arm results in smaller joint moment development, power and work outputs in fast motions. *J. Biomech.* **36**, 1675-1681.
- Roberts, T. J. (2002). The integrated function of muscles and tendons during locomotion. *Comp. Biochem. Physiol. A* **133**, 1087-1099.
- Roberts, T. J. and Marsh, R. L. (2003). Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *J. Exp. Biol.* **206**, 2567-2580.
- Rolian, C., Lieberman, D. E., Hamill, J., Scott, J. W. and Werbel, W. (2009). Walking, running and the evolution of short toes in humans. *J. Exp. Biol.* **212**, 713-721.
- Rosager, S., Aagaard, P., Dyhre-Poulsen, P., Neergaard, K., Kjaer, M. and Magnusson, S. P. (2002). Load-displacement properties of the human triceps surae aponeurosis and tendon in runners and non-runners. *Scand. J. Med. Sci. Sports* **12**, 90-98.
- Rugg, S. G., Gregor, R. J., Mandelbaum, B. R. and Chiu, L. (1990). In vivo moment arm calculations at the ankle using magnetic resonance imaging (MRI). *J. Biomech.* **23**, 495-501.
- Sacks, R. D. and Roy, R. R. (1982). Architecture of the hind limb muscles of cats: functional significance. *J. Morphol.* **173**, 185-195.
- Scholz, M. N., Bobbert, M. F., van Soest, A. J., Clark, J. R. and van Heerden, J. (2008). Running biomechanics: shorter heels, better economy. *J. Exp. Biol.* **211**, 3266-3271.
- Schutte, L. M. (1992). Using musculoskeletal models to explore strategies for improving performance in electrical stimulation-induced leg cycle ergometry: Stanford University.
- Smith, N. C., Payne, R. C., Jespers, K. J. and Wilson, A. M. (2007). Muscle moment arms of pelvic limb muscles of the ostrich (*Struthio camelus*). *J. Anat.* **211**, 313-324.
- Spector, S. A., Gardiner, P. F., Zernicke, R. F., Roy, R. R. and Edgerton, V. R. (1980). Muscle architecture and force-velocity characteristics of cat soleus and medial gastrocnemius: implications for motor control. *J. Neurophysiol.* **44**, 951-960.
- Ward, S. R., Eng, C. M., Smallwood, L. H. and Lieber, R. L. (2009). Are current measurements of lower extremity muscle architecture accurate? *Clin. Orthop. Relat. Res.* **467**, 1074-1082.
- Williams, P. E. and Goldspink, G. (1978). Changes in sarcomere length and physiological properties in immobilized muscle. *J. Anat.* **127**, 459-468.
- Williams, S. B., Wilson, A. M., Daynes, J., Peckham, K. and Payne, R. C. (2008). Functional anatomy and muscle moment arms of the thoracic limb of an elite sprinting athlete: the racing greyhound (*Canis familiaris*). *J. Anat.* **213**, 373-382.
- Zajac, F. E. (1989). Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. *Crit. Rev. Biomed. Eng.* **17**, 359-411.
- Zumwalt, A. (2006). The effect of endurance exercise on the morphology of muscle attachment sites. *J. Exp. Biol.* **209**, 444-454.