

This item was submitted to [Loughborough's Research Repository](#) by the author.
Items in Figshare are protected by copyright, with all rights reserved, unless otherwise indicated.

The muscle morphology of elite sprint running

PLEASE CITE THE PUBLISHED VERSION

<https://doi.org/10.1249/MSS.0000000000002522>

PUBLISHER

American College of Sports Medicine (ACSM)

VERSION

AM (Accepted Manuscript)

PUBLISHER STATEMENT

This paper was accepted for publication in the journal *Medicine and Science in Sports and Exercise* and the definitive published version is available at <https://doi.org/10.1249/MSS.0000000000002522>.

LICENCE

CC BY-NC-ND 4.0

REPOSITORY RECORD

Miller, Robert, Thomas G Balshaw, Garry J Massey, Sumiaki Maeo, Marcel B Lanza, Michael Johnston, Sam Allen, and Jonathan Folland. 2020. "The Muscle Morphology of Elite Sprint Running". Loughborough University. <https://hdl.handle.net/2134/13078007.v1>.

The Muscle Morphology of Elite Sprint Running

Original Investigation

Robert Miller^{1,2}, Thomas G. Balshaw¹, Garry J. Massey³, Sumiaki Maeo⁴, Marcel B. Lanza⁵, Michael Johnston^{2,6}, Sam J. Allen¹, Jonathan P. Folland¹

¹School of Sport, Exercise and Health Sciences, Loughborough University, UK

²British Athletics, Loughborough University, UK

³School of Sport and Health Sciences, University of Exeter, Devon, UK

⁴Research Organization of Science and Technology, Ritsumeikan University, Kusatsu, Shiga, Japan

⁵Department of Physical Therapy and Rehabilitation, University of Maryland Baltimore, Baltimore, United States

⁶Applied Sports Technology Exercise and Medicine Research Centre, Swansea University, UK

Address for Correspondence:

Jonathan P. Folland, Ph.D

School of Sport, Exercise and Health Sciences, Loughborough University, Leicestershire, LE11 3TU, United Kingdom

Tel: +44 (0)1509 226 334

E-mail: J.P.Folland@lboro.ac.uk

Title Character Count: 45

Abstract word count: 274

Number of figures and tables: 3 figures, 3 tables.

ABSTRACT

The influence of muscle morphology and strength characteristics on sprint running performance, especially at elite level, is unclear. **Purpose:** This study aimed to investigate the differences in muscle volumes and strength between male elite sprinters, sub-elite sprinters, and untrained controls; and assess the relationships of muscle volumes and strength with sprint performance. **Methods:** Five elite sprinters (100 m seasons best [SBE_{100}]: 10.10 ± 0.07 s), 26 sub-elite sprinters (SBE_{100} : 10.80 ± 0.30 s) and 11 untrained control participants underwent: 3T magnetic resonance imaging scans to determine the volume of 23 individual lower limb muscles/compartments and 5 functional muscle groups; and isometric strength assessment of lower body muscle groups. **Results:** Total lower body muscularity was distinct between the groups (controls < sub-elite +20% < elite +48%). The hip extensors exhibited the largest muscle group differences/relationships (elite, +32% absolute and +15% relative [per kg] volume vs sub-elite; explaining 31-48% of the variability in SBE_{100}), whereas the plantarflexors showed no differences between sprint groups. Individual muscle differences showed pronounced anatomical specificity (elite vs sub-elite, absolute volume range +57% to -9%). Three hip muscles were consistently larger in elite vs. sub-elite (TFL, sartorius, gluteus maximus; absolute +45-57% and relative volume +25-37%), and gluteus maximus volume alone explained 34-44% of the variance in SBE_{100} . Isometric strength of several muscle groups was greater in both sprint groups than controls, but similar for the sprint groups and not related to SBE_{100} . **Conclusions:** These findings demonstrate the pronounced inhomogeneity and anatomically specific muscularity required for fast sprinting, and provides novel, robust evidence that greater hip extensor and gluteus maximus volumes discriminate between elite and sub-elite sprinters and are strongly associated with sprinting performance.

Key Words: Sprinting, muscle volume, isometric strength

INTRODUCTION

Sprint running, including the ability to accelerate quickly and achieve high maximum running speeds, is one of the most revered and long-standing expressions of human athletic performance and is considered a key component of numerous running-based sports. Elite sprinters are capable of achieving impressive gait speeds of over 12 m.s⁻¹ (1), due to the generation of extremely high muscular power, particularly from the major muscle groups of the lower body. Theoretically, neuromuscular power is largely determined by muscle volume, and empirical evidence has demonstrated very strong relationships between muscle volume and neuromuscular power of single muscle groups (2). This suggests that muscle volume may be of critical importance for sprint performance, and whilst it is a common observation that elite sprinters are typically more muscular than untrained populations, the specific muscle groups important for elite sprint running performance remain unclear.

The ‘gold-standard’ method of measuring muscle volume is magnetic resonance imaging (MRI; [(3)]), however, to date only a small number of studies have used MRI to investigate the importance of muscle volumes for sprint running performance. Recent evidence supports the notion that sprinters are generally more muscular (i.e. greater muscle volume) than non-sprinters (controls), but with a non-uniform pattern of muscular hypertrophy such that the hip and biarticular hip and knee joint muscles appear to be larger, whereas the monoarticular knee joint muscles and muscles of the lower leg may be more similar (4, 5). Moreover, there are also suggestions that the volume of specific muscles could be related to sprint performance, although with considerable confusion about which muscles / muscle groups may be most important; for example there are reports that psoas major (6-8); rectus femoris (4); adductors (8, 9); hamstrings (7, 9); quadriceps (8), or even ratios of muscle volumes (psoas major:quadriceps [10]; gluteus maximus:quadriceps [7]) may be most important. This

confusion may have arisen as most studies have examined only a limited and variable number of muscles or muscle groups (7-11) rather than a complete analysis of the lower body musculature.

Importantly, comparisons to date have also been limited to sprinters vs. controls (4, 5) or sprinters vs. endurance runners (9), rather than what distinguishes elite from sub-elite sprinters. This is because previous studies have not included athletes that are genuinely elite (i.e. internationally competitive) with the fastest personal best 100 m times of participants being 10.68 s (11), 10.67 s (4), 10.23 s (7), 10.95 s (10), division 1 collegiate level sprinters (performance times undefined; [(5)]), and 13.24 s in preadolescent boys (8). Finally, the number of sprinters assessed has typically been relatively small for quantifying the relationship between sprint performance and muscle volumes (n=8-16; [4, 5, 8, 9, 11]). Thus, no comparison between elite and sub-elite sprinters has yet been made, and the muscle groups that need to be particularly large in order to attain elite running speeds remains to be elucidated.

Similarly, the functional characteristics of specific muscle groups needed for elite sprint running remain largely unknown. Whilst some studies have assessed strength, during multiple joint exercises (e.g. squatting, isometric mid-thigh pull) in relation to acceleration and / or sprint performance of athletic groups (12, 13), this clearly does not allow identification of which specific muscle groups need to be strong / powerful to enable fast running. Whilst it has been speculated that hip flexion and extension strength may be critical for fast running (6, 7), we are aware of only one preliminary study that reported these muscle groups to be stronger in sprinters and largely predictive of sprint performance (14). In fact, to date no studies have done a comprehensive assessment of the strength of a range of ankle,

knee and hip joint muscles in elite and / or sub-elite sprinters as well as untrained controls in order to understand the functional characteristics that may differentiate these groups.

Therefore, the aims of this study were to investigate the differences in muscle volumes and strength between elite sprinters, sub-elite sprinters and untrained controls; and to assess the relationships of both muscle volumes and strength with sprint performance amongst sprinters. It was hypothesised that the hip flexor and extensor muscles would be progressively larger relative to body mass according to group (controls < sub-elite < elite), and be related to sprint performance amongst the whole cohort of sprinters. Additionally, it was postulated that isometric torque of the hip flexor and extensor muscle groups would be different between groups, and related to sprint performance.

METHODS

Participants & Sprint Performance

All of the participants were healthy young men, asymptomatic for leg or back injury, with no minor injury in the previous 4 weeks and no major injury in the previous 6 months. Five elite sprinters (Mean \pm SD; age 27 ± 4 y, body mass 86.4 ± 6.7 kg, height 1.83 ± 0.06 m), 26 sub-elite sprinters (22 ± 2 y, 75.4 ± 7.3 kg, 1.78 ± 0.06 m) and 11 control participants (26 ± 3 y, 75.2 ± 5.6 kg, 1.80 ± 0.08 m; Table 1) volunteered to participate and gave informed consent to take part in this study. Elite sprinters were required to have a season's best 100 m sprint time of <10.25 s (the British Athletics 100 m selection standard for the European Outdoor Championships 2018 [15]). Sub-elite sprinters were required to have a season's best time of 10.35-11.50 s for 100 m or equivalent for 60 m / 200 m based on International Association of Athletics Federations (IAAF) points, and to have completed at least one season of high-intensity sprint-specific training. Participants in both sprint groups completed a minimum of two sprint specific training sessions and one resistance training session per week. Control participants had a low-moderate level of physical activity (i.e. vigorous-intensity activity ≤ 2 x per week, and ≤ 1500 MET-minutes.week⁻¹, overall vigorous and moderate physical activity ≤ 3000 MET-minutes.week⁻¹; [(16)]) and were not involved in systematic physical training or competitive sports (for ≥ 1 year). Season's best and personal best sprint (60 m, 100 m and 200 m) times were taken from the national governing body database (www.thepowerof10.info) of electronically timed races with wind readings (<2.0 m.s⁻¹) during the corresponding calendar year in which data collection took place (season's best); or the athletes career at the end of that season (personal best). Sprint performances were converted to IAAF points, a classification system that allows performance comparisons between different events, and each athletes maximum points in any of the sprint events (60, 100 and 200 m) was taken as their performance measure and converted back into 100 m season's best equivalent (SBE₁₀₀)

or personal best equivalent (PBE₁₀₀) times. For the elite sprint group SBE₁₀₀ (10.10 ± 0.07 , range 10.03 - 10.21 s) and PBE₁₀₀ (9.99 ± 0.07 , range 9.91-10.08 s) were actual 100 m performances for all individuals (i.e. 100 m was their best event). For the sub-elite sprint group SBE₁₀₀ was actual 100m performances for 73% of these athletes (19 out of 26), whilst for seven athletes SBE₁₀₀ was derived from either 60 m or 200 m season's best times. Consequently, the whole sprint cohort had SBE₁₀₀ ranging from 10.03 - 11.50 s (10.71 ± 0.37 s). Ethical approval was granted by the Loughborough University Ethics Approvals (Human Participants) Sub-Committee.

Study Overview

Participants were required to attend two measurement sessions within this cross-sectional study: one for isometric strength measurements and one for assessing muscle morphology (MRI). All measurement sessions were scheduled after a rest day or light training day and participants were instructed to arrive in a relaxed state having followed normal daily activity and dietary behaviours, where they then sat quietly for 15 minutes prior to their MRI scan. Due to limitations in scheduling and practicalities of data collection with elite athletes it was not feasible to control for measurement time of day.

Anthropometry

Body mass was measured using a calibrated ADAM C-150 weighing scale (ADAM equipment, Oxford, CT), and stature was measured using a wall-mounted stadiometer (Holtain Ltd., Crymmych, UK). Skinfold thickness was measured at eight sites (bicep, tricep, subscapular, iliac crest, supraspinale, abdominal, thigh and calf) using Harpenden skinfold callipers (British Indicators Ltd, Wolverhampton, UK), and the averages of two measurements at each site were recorded. Additionally, waist and gluteal circumferences

were collected. All anthropometric measures were done by the same investigator, and in accordance with the International Society for the Advancement of Kinanthropometry guidelines (17). The sum of four skinfolds (bicep, tricep, subscapular and iliac crest) was used to calculate body density using the formula for males aged 20-29 years (18), and percentage body fat estimated using the Siri (19) equation. Fat-free mass was derived from the percentage body fat and body mass values.

Muscle Volume with Magnetic Resonance Imaging

T1-weighted axial magnetic resonance (MR) images of the abdomen, thigh and shank were obtained with a 3T scanner (Discovery MR750w, GE Healthcare, Chicago, IL, USA) with a receiver 8-channel whole-body coil. Images (time of repetition 600 ms, time of echo 8 ms, field of view 450 x 450 mm, image matrix 320 x 320, pixel size 1.4 x 1.4 mm, slice thickness 5 mm, interslice gap 5 mm) were obtained from the twelfth thoracic vertebra to the calcaneus capturing both legs in five overlapping blocks. Subjects were scanned while in the supine position with arms folded across the chest, with hip and knee joints extended and the ankle joint at ~90°. Oil filled capsules were placed in equal segments on the right leg of each participant during scanning, in order to facilitate alignment between the blocks during analysis.

The MR images were manually segmented to assess cross-sectional area (CSA) and derive the volume of 23 lower limb muscles / compartments. Specifically, every other MR image (i.e. 20mm between the centre of the measured images) starting from the most proximal image in which the muscle appeared, were segmented using a public domain DICOM software (Horos, version 2.2.0 www.thehorosproject.org). The average number of images analysed per muscle is shown in Table 2. Six separate investigators carried out the analysis,

with each investigator analysing the same muscles / compartments for the entire cohort, and blinded to participant identity / group. Fully analysed images for each participant (i.e. all 26 muscles/compartments) were then checked and quality assured for accuracy by a single investigator (RM), paying particular attention to errors and overlaps between adjacent muscle cross-sections. The analysed muscles / compartments were: iliopsoas (psoas major and iliacus combined); sartorius; tensor fasciae latae (TFL); adductor magnus; gracilis; gluteus maximus; gluteus medius; gluteus minimus; rectus femoris; vastus lateralis, medialis and intermedius; semimembranosus; semitendinosus; biceps femoris long and short heads; popliteus; lateral and medial gastrocnemius; soleus; and the anterior, lateral and deep posterior compartments of the shank. The shank compartments were the combined volume of the following muscles: tibialis anterior, extensor digitorum longus and extensor halluc longus, (anterior); peroneous longus and brevis (lateral); plantaris, tibialis posterior, flexor digitorum longus, flexor halluc longus (deep posterior). The volume of five functional muscle groups were calculated as the sum of the following muscles; hip extensors (gluteus maximus, adductor magnus, biceps femoris long head, semimembranosus and semitendinosus); hip flexors (iliopsoas, rectus femoris, sartorius, TFL); knee extensors (rectus femoris, vastus intermedius, medialis and lateralis); knee flexors (gracilis, biceps femoris long and short head, semimembranosus, semitendinosus, sartorius, popliteus and medial and lateral gastrocnemius); and plantarflexors (medial and lateral gastrocnemius and soleus).

The volume of each muscle (V_m) was calculated using previously outlined methods (7):

$$V_m = \sum_{i=1}^{n-1} \frac{h}{2} (Am_i + Am_{i+1})$$

where A_m represents the muscle cross sectional area calculated from each image, i is the image number, n is the total number of images, and h is the distance between images (20 mm). In addition to absolute muscle volume (cm^3), muscle volume was also expressed relative to body mass ($\text{cm}^3 \cdot \text{kg}^{-1}$).

Strength Measurements

Isometric strength of the five functional muscle groups were assessed with custom-built isometric dynamometers in the following order (for reference hip [180°], knee [180°] and ankle [90°] angles in the anatomical position; flexion is lower): hip extensors (upper body prone, hip 145°, knee 150°); hip flexors (upper body supine, hip 180°, knee 150°); knee extensors (sitting, hip 115°, knee 120°); knee flexors (upper body prone, hip 150°, knee 150°); and plantarflexors (sitting, hip 110° knee 180°, ankle 100°). Measurements were made unilaterally, first with the right leg then the left, before moving to the next dynamometer. Participants were tightly secured to each dynamometer using extensive strapping in order to minimise extraneous movement. During extension and flexion of the hip and knee, a calibrated S-shaped strain gauge (linear response up to 2000 N) and specific braces were positioned in the movement plane perpendicular to the long axis of femoral / tibial movement and strapped 4 cm proximal to the knee / ankle joints, respectively. During plantarflexion contractions force data was collected using a portable Kistler force plate (Type 9602A, Kistler Instruments Corp, Winterthur, Switzerland) mounted to a custom-built rig. For all isometric measurements, the force signal was amplified (x500), interfaced with an analogue to digital converter (CED micro 1401, CED, Cambridge, UK) and sampled at 2000 Hz with a personal computer using Spike 2 software (CED, Cambridge, UK).

With each dynamometer and muscle group, participants first completed a standardised series of warm-up contractions, each of 3 s duration with 15 s rest in-between (3 x 50%, 3 x 75%, 1 x 90% perceived maximum) followed by at least two subsequent maximal voluntary contractions of the relevant muscle group, lasting ~4 s with at least 60 s rest in between. A third contraction was completed if the participant scored higher on their second contraction than the first. During the maximal contractions, participants were given strong verbal encouragement, instructed to push as hard as possible for the duration of the contraction, and were provided with real-time biofeedback displayed on a computer monitor with a target cursor representing their maximum force in preceding contractions. Maximal voluntary force (MVF) was the highest instantaneous force achieved, corrected for the force due to gravity (i.e. baseline force at rest), and maximal voluntary torque (MVT) was calculated as the product of MVF and measured lever length (m). For the hip and the knee muscle groups lever length was manually measured as the distance between the centre of the strap and the centre of rotation of the respective joint. In order to calculate plantarflexion lever length, sagittal plane video was recorded synchronous to the force measurement at 60 Hz during the MVCs with a camera (Panasonic, HC-V110, Kadoma, Japan) placed 4 m perpendicular to the movement plane, with the field of view maximised with optical zoom and markers on the knee joint, lateral malleolus and the lateral head of the fifth metatarsal. The corners of the force plate and ankle location were manually digitised and ankle torque was calculated as the perpendicular distance from the normal force vector to the ankle joint centre, multiplied by the magnitude of the normal force vector.

Statistical Analysis

Muscle volume and strength measurements assessed on both legs were averaged to provide unilateral criterion values for each participant. Data are presented as mean \pm standard

deviations (SD). The Shapiro-Wilk test was used to assess the normality of distribution, and revealed that >90% of the variables were normally distributed, in which case we used parametric statistical tests to provide a consistent approach. One-way ANOVA and subsequent Bonferroni post-hoc analysis were used to assess differences between groups for muscle volume (absolute, and relative to body mass), torque (absolute, and relative to body mass) and anthropometry. Statistical significance was set at $P < 0.05$. For the whole cohort of sprinters (i.e. elite and sub-elite groups combined, not including the control group) the bivariate relationships between SBE_{100} and measures of muscle volume and strength were assessed using Pearson's product moment correlation. Correlation coefficients were categorised as 'weak' ($r \leq 0.40$), 'moderate' ($r = 0.40-0.60$), 'strong' ($r = 0.60-0.80$) or 'very strong' ($r = 0.8-1.0$). Correlation P values were corrected for multiple tests using the Benjamini-Hochberg (20) method with a false discovery rate of 5% and the significance level was defined as adjusted $P < 0.05$. Stepwise multiple linear regression was used to calculate the variance in SBE_{100} explained by the best combination of variables in each of the following categories: absolute and relative muscle volume of individual muscles and muscle groups. In practice based on their significant bivariate correlations with SBE_{100} the following were entered into four distinct regression analyses for each of these categories of variables: (i) absolute volume of muscle groups (5 muscle groups); (ii) absolute muscle volume of individual muscles (18 specific muscles); (iii) relative volume of muscle groups (2 muscle groups); (iv) relative volume of individual muscles (1 specific muscle). All statistical procedures were performed with IBM SPSS Statistics Version (IBM Corp., New York, N, USA).

RESULTS

Anthropometrics

Elite sprinters were similar in stature, but heavier (>10 kg) than both sub-elite sprinters and untrained controls ($P=0.006$ and $P=0.013$ respectively; Table 1). Both sprint groups had a lower percentage body fat and sum of 8 skinfolds compared with controls ($P\leq 0.01$). Fat free mass was greater in elite sprinters than both sub-elite sprinters (>12 kg, $P\leq 0.01$) and controls (>16 kg, $P\leq 0.01$).

****Insert Table 1 here****

Comparison of Absolute Muscle Volumes

Total unilateral volume of all the measured muscles was greater for both sprint groups vs. controls (elite $+48\%$; sub-elite $+20\%$; both $P<0.01$) and for the elite vs. sub-elite sprinters ($+24\%$; $P=0.01$; Table 2). Elite sprinters had greater absolute muscle volume than sub-elite sprinters for four functional muscle groups (hip extensors $+32\%$; knee flexors $+24\%$; hip flexors $+23\%$; knee extensors $+22\%$; All $P\leq 0.01$; Figure 1), but not the plantarflexors. Compared to controls, sub-elite sprinters had greater muscle volume of four functional muscle groups ($+20-34\%$, $P\leq 0.009$; except the plantarflexors; See Figure, Supplemental Digital Content 1, Percentage differences in absolute and relative muscle volumes between sub-elite sprinters vs. controls). The functional muscle groups and individual muscles are ordered according to the magnitude of the percentage differences for absolute muscle volume), and elite sprinters were larger in all 5 functional muscle groups ($+29-77\%$, all $P\leq 0.020$). When comparing absolute volume of individual muscles / compartments between groups there were non-uniform differences and pronounced anatomical specificity e.g. elite vs sub-elite sprinters ranging from $+57\%$ (TFL) to -9% (lateral compartment of the shank).

Eight individual muscles were larger in elite vs sub-elite sprinters (all $P \leq 0.035$): TFL (+57%), sartorius (+47%), gluteus maximus (+45%), adductor magnus (+28%), semitendinosus (+28%), biceps femoris long head (+27%), vastus medialis (+24%) and vastus intermedius (+22%). Furthermore, compared to controls, elite sprinters had 15 out of 23 muscles / compartments that were larger (+36-106%, $P \leq 0.018$), and sub-elite sprinters had 10 muscles / compartments that were larger (+19-60%, $P \leq 0.019$). In summary, for absolute muscle volumes, similar differences were noted for the two comparisons between sub-elite sprinters vs. controls and elite vs. sub-elite sprinters (See Table, Supplementary Digital Content 2, A summary table of the observed significant differences between sub-elite sprinters vs. controls, and elite sprinters vs. sub-elite sprinters).

****Insert Table 2 here****

Comparison of Relative Muscle Volumes

Regarding relative muscle volume, total volume of the measured muscles was greater for both sprint groups vs. controls (elite +29%, $P < 0.001$; sub-elite +20%, $P = 0.001$), but with no differences between the sprint groups ($P = 0.107$). The hip extensors were the only muscle group to differentiate elite from sub-elite sprinters based on relative muscle volume (+15%, $P = 0.003$), and the only individual muscles that had larger relative muscle volume in the elite vs. sub-elite sprinters were the gluteus maximus (+25, $P \leq 0.001$), sartorius (+28%, $P = 0.013$), and tensor fasciae latae (+37%, $P = 0.032$). Compared to controls, both sprint groups had greater relative muscle volume of the flexors and extensors of the hip and knee (i.e. four muscle groups; +20-54%, all $P \leq 0.001$), but there were no differences for the plantarflexors. Additionally, in comparison to controls the sprint groups had 13 (elite sprinters, +24-77%) and 12 (sub-elite sprinters, +16-58%) larger individual muscles relative to body mass. In

summary, for relative muscle volumes, whilst there were many differences between sub-elite sprinters vs. controls, there were far fewer differences between elite vs. sub-elite sprinters (See Table, Supplementary Digital Content 2, A summary table of the observed significant differences between sub-elite sprinters vs. controls, and elite sprinters vs. sub-elite sprinters).

****Insert Figure 1 here****

Relationships between Sprint Performance and Muscle Volumes

Amongst the whole sprint cohort, SBE₁₀₀ showed moderate to strong correlations with absolute muscle volume of all the muscles combined ($r=-0.629$, $P<0.001$), each of the five muscle groups ($r=-0.495$ to -0.689 , $P\leq 0.05$, Table 3), as well as 18 out of 23 individual muscles / compartments ($r=-0.409$ to -0.662 ; All $P\leq 0.05$) i.e. only five individual muscles were not correlated with SBE₁₀₀. The highest correlations of absolute muscle volumes with SBE₁₀₀ for any muscle group was the hip extensors ($r=-0.689$, $P<0.001$) and for any individual muscle was the gluteus maximus ($r=-0.639$, $P<0.001$; Figure 2). Relative to body mass, the combined volume of all the muscles ($r=-0.422$, $P=0.036$), two muscle groups (hip extensors $r=-0.560$, $P=0.005$; and knee flexors $r=-0.522$, $P=0.006$) and only one individual muscle (gluteus maximus $r=-0.580$, $P=0.014$) were moderately associated with SBE₁₀₀ (Figure 2). Two further individual muscle volumes relative to body mass, however, displayed a tendency to be moderately related to SBE₁₀₀ (sartorius $r=-0.484$, $P=0.066$; TFL $r=-0.454$, $P=0.079$). The regression models revealed that only the single strongest predictor variable contributed to the explained variance in SBE₁₀₀ within each category of predictor variables: absolute volume of muscle groups, hip extensors explained 47.5% of the variance in SBE₁₀₀; relative volume of muscle groups, hip extensors explained 31.4% of the variance; absolute

volume of individual muscles, gluteus maximus explained 43.8% of the variance, relative volume of individual muscles, gluteus maximus explained 33.6% of the variance.

****Insert Table 3 and Figure 2 here****

Isometric Strength

Sub-elite sprinters had greater absolute strength of the knee extensors (+26%, $P=0.001$) and flexors (47%, $P=0.005$) compared to controls, but with no differences in any other muscle groups. Elite sprinters showed a distinct pattern of differences compared to controls with greater absolute strength of the hip flexors (+55%, $P=0.002$) and extensors (+63%, $P=0.002$), and knee flexors (+62%, $P=0.013$; Figure 3). When relative torque was compared, sub-elite sprinters outperformed controls across all muscle groups (mean difference +34%, $P\leq 0.027$). Similar to absolute torque, the elite group produced greater relative torque than the controls during hip extension (+48%, $P=0.002$), hip flexion (+40%, $P=0.007$) and knee flexion (+49%, $P=0.049$) than the controls. However, there were no differences observed in absolute or relative torque between elite and sub-elite sprinters across any of the five muscle groups (Figure 3).

Absolute strength of all five muscle groups was unrelated to sprint performance. For relative strength, counterintuitively one muscle group, relative knee extensor strength, was positively correlated with SBE_{100} ($r= 0.485$, $P=0.033$; i.e. greater knee extension torque, slower sprint time), but there were no relationships for other muscle groups ($r= -0.265$ to 0.139 , $P>0.105$).

****Insert Figure 3 here****

DISCUSSION

The aim of this study was to compare the lower body muscle volumes and strength characteristics between a group of genuinely elite sprinters with sub-elite sprinters and untrained controls; and to assess the relationships of these measures with sprint performance amongst sprinters. MRI analysis revealed total lower body muscularity was distinct between all three groups (vs. controls: sub-elite +20%, elite +48%), such that the elite sprinters had ~3.7 kg and ~2.2 kg of extra muscle mass per leg than controls and sub-elite sprinters respectively. However, the differences in muscle volume between the groups were highly non-uniform with substantial anatomical specificity according to muscle group and especially individual muscle. For elite vs sub-elite sprinters, the largest muscle group specific effects were found primarily for the hip extensors (differences of +32% absolute and +15% relative volume; explaining 47.5% [absolute volume] to 31.4% [relative volume] of the variability in performance) and secondarily for the knee flexors (differences of +24% absolute volume; performance correlations for absolute [$r=-0.682$] and relative [$r=-0.522$] volume), whereas the plantarflexors showed no differences between the sprint groups. Individual muscles showed even greater anatomical specificity with three muscles being larger in elite vs. sub-elite sprinters in both absolute and relative terms (TFL, absolute +57%, relative +37%; sartorius, absolute, +47%, relative +28%; gluteus maximus, absolute +45%, relative +25%) and the gluteus maximus alone explained 33.6% (relative volume) to 43.8% (absolute volume) of the variance in performance amongst sprinters. Whilst both sprint groups had stronger hip and knee muscle groups than controls, isometric strength did not differentiate between sprint groups and was unrelated to sprint performance. Therefore, this study provides novel and robust evidence highlighting the importance of specific morphological characteristics, principally hip extensor and gluteus maximus volume, for elite sprint running.

For the control group in this study, both muscle volume and knee joint muscular strength were comparable to previously published investigations utilising similar measurements in analogous populations (21-23). Both sprint groups demonstrated relatively large muscle volumes when compared with previous studies, however comparison to previous literature is confounded by differences in performance standard, the inclusion of both male and female sprinters in some studies (5) and potential ethnic differences (7). The performance standard of the elite sprinters in this study ($n=5$; SBE_{100} 10.03 – 10.21 s; PBE_{100} 9.91 – 10.08 s) were all faster than any previously studied individual sprinter or cohort (e.g. fastest personal best 10.23 – 11.71 s [4, 7, 9]). The sub-elite group in the current study (PBE_{100} : 10.34 – 11.24 s) were of a comparable, if not higher, performance standard to previous research. Hence this appears to be the first comprehensive comparison of muscle morphology and strength between genuinely elite sprinters with sub-elite sprinters and controls.

Absolute Muscle Volume

Preliminary anthropometrics revealed the three groups had similar stature and BMI, but both sprint groups were leaner than controls and the elite group were heavier (>11 kg) and had greater FFM (>13 kg) than both the other groups. From the MRI analysis, total muscle volume of all the muscles was distinct and progressively larger according to sprint performance (controls $<$ sub-elite $+20\%$ $<$ elite $+48\%$) with elite sprinters having ~ 4.4 kg (vs sub-elite) and ~ 7.4 kg (vs controls) of extra muscle mass across both legs. These differences in lower limb muscularity are in accordance with, but more pronounced than, previous studies of sub-elite sprinters (5, 7). The mechanistic reason for the greater muscularity of elite $>$ sub-elite $>$ controls in the current study, are not possible to discern from this investigation, although it seems likely that the sprint and resistance training history of the groups, which shows a similar pattern, would contribute to these differences in muscularity.

405

406 Furthermore, there was extensive anatomical variability in the magnitude of differences
407 between muscle groups and particularly individual muscles / compartments. Specifically
408 there were differences between all 3 groups (elite>sub-elite>controls) for 4 out of 5 muscle
409 groups, with the greatest differences in hip extensors (sub-elite +34%; elite +77% vs
410 controls) followed by the knee flexors (+27%; +58%), hip flexors (+27%; +57%) and knee
411 extensors (+20%; +46%), whereas only the elite sprinters > controls for the plantarflexors
412 (+29%). The broad pattern of these findings, with the largest differences in the hip and knee
413 joint muscles, but less pronounced differences for the ankle joint muscles is in accordance
414 with previous research comparing sub-elite sprinters vs. non-sprinters (4, 5). The current
415 study has extended those findings, with elite runners found to have particularly pronounced
416 muscularity of the hip extensors and flexors, and knee flexors, and thus to our knowledge this
417 is the only research study to date highlighting the morphological characteristics important for
418 elite level sprinting. At running speeds $> 7.5 \text{ m.s}^{-1}$ there appears to be a disproportionate
419 requirement for power generation by the hip flexors, hip extensors and knee flexor muscle
420 groups (24). Biomechanically the hip extensors are primarily responsible for the back swing
421 of the legs during stance (25), and both the hip extensor and knee flexors facilitate the
422 application of horizontal forces to the ground (26), and thus these muscle groups are
423 considered critical for propulsion (27). Whereas, the hip flexors are thought crucial to the
424 rapid acceleration of the legs during swing phase in order to achieve high stride frequencies
425 (24, 28). From this perspective it is logical that elite sprinters would be larger in these muscle
426 groups.

427

428 Individual muscle differences between the groups showed pronounced anatomical specificity
429 with the muscles of elite vs. sub-elite sprinters ranging from +57% (TFL) to -9% (lateral

compartment of the shank). Elite sprinters had 8 out of 23 larger muscles / compartments vs. sub-elite (+22-57%: TFL, sartorius, gluteus maximus, semitendinosus, adductor magnus, biceps femoris long head, vastus intermedius and vastus medialis) and with 6 of these being hip muscles. Furthermore, both sprint groups had 10 (sub-elite +20-47%) and 15 (elite +35-115%) larger muscles / compartments than controls. Strikingly, amongst the sprinters total muscle volume, the volume of all five muscle groups and 18/23 individual muscles were all found to be related to SBE_{100} (i.e. greater volume, faster sprint time). However, strong relationships ($r > 0.60$), and in fact the highest correlations in this study, were observed between SBE_{100} and volume of the hip extensor ($r = -0.689$) and knee flexor muscle groups ($r = -0.682$) as well as two constituent muscles from within these groups (gluteus maximus $r = -0.662$; and sartorius $r = -0.639$). The largest previous study of muscle morphology in sub-elite sprinters also reported the absolute volume of 4/12 individual muscles, including the gluteus maximus and hamstrings, to be related to 100 m time ($r = 0.37-0.42$; [(7)]). Inclusion of elite level sprinters in the current investigation and the somewhat higher average performance standard of our cohort (10.71 vs 10.94 s [(7)]) might explain the more pronounced relationships we have found. Subsequently, regression analyses revealed that absolute volume of the hip extensors explained 47.5%, and gluteus maximus 43.8% of the variance in sprint running performance, respectively. Given the multifactorial nature of sprint running performance, widely considered to depend on an array of anatomical, biomechanical, physiological, technical and psychological variables (29), the apparent importance of these specific muscle morphology characteristics in explaining >40% of the variance in performance is remarkable.

Overall, these findings highlight the importance of the absolute size of specific muscle groups (primarily the hip extensors and secondarily knee flexors) and muscles (gluteus

maximus and sartorius) for sprint performance. The consistency of our findings / differences between both sub-elite sprinters vs. controls and elite sprinters vs. sub-elite sprinters for absolute muscle volumes (See Table, Supplemental Digital Content 2, A summary table of the observed significant differences between sub-elite sprinters vs. controls, and elite sprinters vs. sub-elite sprinters), and the most distinct muscle groups / muscles explaining substantial proportions of the variance in sprint performance, reinforces the apparent veracity of these findings. The primary importance of the hip extensors (the largest muscle group differences for both elite vs. sub-elite, +32%; and sub-elite vs. controls, +34%; explaining 47.5% of the variance in SBE₁₀₀) and gluteus maximus (greater for both elite vs. sub-elite, +45%; and sub-elite vs. controls, +35%, explaining 43.8% of the variance in SBE₁₀₀) are original findings. Previous literature have reported contradictory findings for the primary importance of various muscle groups and muscles (4, 6, 8-10), without highlighting the importance of the hip extensors and gluteus maximus. These investigations typically used smaller numbers of sprinters (n= 8-16) of sub-elite sprinters (fastest individual 100 m personal best = 10.33 s), and have performed less comprehensive morphological analyses (i.e. a limited number of lower body muscles). As discussed above, given the key role of the hip extensors and gluteus maximus in propulsion (25, 26), it is surprising that until now there has been little empirical evidence to support their importance for sprint running performance.

The importance of absolute muscularity would certainly be expected to be beneficial for absolute power production given the strong association of these variables ($R^2 \sim 0.80$; [2]), but may be surprising given that sprint running has often been considered to depend on power per unit body mass (i.e. relative muscle volume; [30]). However, theoretical analysis has shown that among runners of similar stature, having greater absolute muscle mass is also biologically necessary in order to attain faster sprinting speeds (31). The current experiment

adds to the data indicating that absolute muscularity, particularly of key muscle groups and individual muscles, is highly important for sprint running performance. Whilst it seems unlikely, an alternative possibility is that the elite sprinters in this study were coincidentally larger and therefore the apparent abundance of differences between groups and associations with sprint performance we have observed for absolute muscle volumes could be an artefact of their coincidentally greater body mass. In this case, relative muscle volume (per kg) facilitates body mass independent comparisons, without this potential confounding difference in body mass between the groups.

Relative Muscle Volume

Relative muscle volume was greater for both sprint groups compared to controls for the flexors and extensors of the hip and knee. For individual muscles the differences in relative muscle volume also showed marked anatomical variability / specificity between the three groups (e.g. elite vs. sub-elite, range +37% TFL to -21% lateral compartment of the shank). Interestingly however only one muscle group (hip extensors; +15%) and three individual muscles (gluteus maximus; +25%, sartorius; +28%, TFL; +37%) were larger in the elite vs. sub-elite sprinters. The TFL and the sartorius have been highlighted as having large differences in volume between sprinters and controls (5), but this is the first study where these muscles have been found to be relatively larger in elite vs. sub-elite sprinters Whilst these muscles have received very little attention to date with regards to their influence on sprint performance, both the TFL and sartorius are key contributors to hip flexion (32). In addition, the sartorius is the only simultaneous knee and hip flexor (33), an important combination of actions in changing limb momentum from down and back at the end of stance, to upwards and forwards during swing, and therefore may be important for early swing phase mechanics and thus sprint performance (5, 25).

Furthermore, strong relationships were observed between SBE_{100} and relative muscle volume of the hip extensor ($r = -0.560$) and knee flexor ($r = -0.522$) muscle groups, and specifically in only one individual muscle (gluteus maximus $r = -0.580$). Consequently, separate regression analyses for muscle groups and individual muscles revealed that the relative volume of the hip extensors explained 31.4%, and gluteus maximus 33.6% of the variance in sprint performance, respectively. During sprint running the gluteus maximus is activated from late swing phase to mid-stance (26), accelerating the leg underneath the body (34) and making a major contribution to the generation of propulsive forces along with the hamstring muscles (26, 35). Thus, greater gluteus maximus volume would be expected to facilitate greater propulsion forces, and therefore greater sprinting speeds. It is interesting that the gluteus maximus, the largest individual muscle in the human body, appears to be particularly important for fast running. The biologically expensive process of developing a large gluteus maximus represents a significant evolutionary investment that presumably confers an advantage for survival. It is possible that the role of the gluteus maximus in facilitating humans to run fast explains the evolution of the gluteus maximus as the largest muscle in the human body.

Isometric Strength

The elite sprinters (absolute and relative 3/5 muscle groups [hip extensors and flexors, and knee flexors] and sub-elite sprinters (absolute 2/5 [knee flexors and extensors]; relative 5/5 muscle groups) were stronger than controls. Due to the observed sprint and resistance training history of the sprint groups, and their greater muscle volume, it is unsurprising that both sprint groups were found to be stronger than controls in a number of muscle groups. Unexpected findings of this study were that no strength measurements for any muscle group

were discriminatory between sprint groups or negatively associated with sprint performance. This contrasts with previous research demonstrating that measures of isokinetic hip flexion strength were related to aspects of sprint performance (14). Furthermore, the speculated importance of hip extension and plantarflexion force during the stance phase (24, 26) and hip flexion force during swing phase (24, 28) for fast running, might also make the current results surprising. However, task / contraction specificity may be an important factor influencing the association between strength / power of the hip muscles and sprint performance (6). Therefore, the findings of this study could be a consequence of a lack of specificity between the isometric strength measures of the current study and the dynamic nature of sprint running (36). It is acknowledged however, that isometric strength was only measured on one occasion and with no familiarisation, due to the difficulty in recruiting elite level sprinters for even a single assessment session. Whilst the protocol was clearly the same for all three groups, this may have introduced some noise into the data potentially, reducing the likelihood of finding more subtle differences between groups, especially given the small sample size of the elite sprint group ($n=5$).

No strength measures were found to be related to faster sprint performance, although a counter-intuitive finding was the positive relationship between relative knee extensor strength and SBE_{100} ($r= 0.485$; i.e. the greater the torque, the slower the sprint time). Previous contrary reports include a negative correlation (37) or no relationship (38) between knee extensor strength and sprint performance in team sports players, rather than the elite level and the sub-elite sprinters of the current study. In addition, work by Dorn and colleagues (24) found that the force requirement of the vastii plateaus as running velocity increases past 5 $m.s^{-1}$, perhaps suggesting that knee extensor torque is not a particular limitation of fast running.

Limitations

There are some limitations associated with the present investigation. First, for some of the sub-elite sprinters (7/26) SBE_{100} was an estimation based on their superior IAAF points at either 60 or 200 m, and as such may have overestimated their 100 m performance. However, the difference in group sprint performance time as a result of this estimation was trivial, and this method ensured that the best sprint performance for each individual was used consistently. Second, there was a temporal separation between the performance (i.e. SBE_{100}) and the laboratory morphology and strength measurements within this study. Whilst this is clearly a potential confounder that might have reduced the strength of the effects we have observed, the continuity of training in the sprint groups would have reduced the likelihood of large differences in muscle volume or strength between the dates of laboratory assessment and sprint performance. Third, it may be argued that the use of isometric force lacks specificity in relation to sprint running (39), where the joint angular velocities can be very high (e.g. knee extension at ~ 850 $^{\circ}/s$ [(1)]). However, the aim of the current study was to accurately assess the isolated strength of five distinct functional muscle groups (i.e. individual joint torques), given the paucity of data on the function, and particularly comparative strength, of these muscle groups in sprinters vs. controls. Isometric measurements are also known to be highly reliable, sensitive and relatively easy to conduct, and also require limited familiarisation time (36), whereas performing these isolated muscle group measurements dynamically, especially at high velocity, in a consistent and reliable manner would be highly challenging. Finally, the cross-sectional nature of this study means that definitive cause and effect relationships remain unknown. However, on the basis of the pronounced differences and relationships we have observed, and the logical rationale for the importance of the muscle groups (hip extensors, knee flexors) and individual muscles

(gluteus maximus) identified, it seems likely that there is a large causal component to these relationships.

Practical Summary and Implications

The extensive differences in muscle morphology between elite and sub-elite sprinters and the strength of the relationships we have observed have clear implications for coaches and practitioners. Whilst overall muscularity appeared important for performance (All muscles: absolute volume +24% for elite vs sub-elite; performance correlations for absolute [$r=-0.629$] and relative [$r=-0.422$] volume), this belied the fact that there were highly variable and non-uniform effects for specific muscle groups and muscles. The largest muscle group specific effects were found primarily for the hip extensors (differences of +32% absolute and +15% relative volume; explaining 47.5% [absolute volume] to 31.4% [relative volume] of the variability in performance) and secondarily for the knee flexors (differences of +24% absolute volume; performance correlations for absolute [$r=-0.682$] and relative [$r=-0.522$] volume), whereas the plantarflexors showed no differences between the sprint groups. This evidence strongly supports the idea that developing large hip extensors and knee flexors, for example through resistance training, would be valuable for the sprint athlete looking to enhance performance (27).

For absolute muscle volumes very similar factors differentiated both sub-elite sprinters from controls as well as elite vs. sub-elite sprinters (e.g. total muscle volume, four muscle groups in the same order of magnitude, and five individual muscles; See Table, Supplemental Digital Content 2, A summary table of the observed significant differences between sub-elite sprinters vs. controls, and elite sprinters vs. sub-elite sprinters), indicating progressive development of these same variables may continuously improve performance up to elite

level. In contrast, for relative volumes, whilst a wide range of factors distinguished sub-elite sprinters from controls, elite sprinters were differentiated by only four variables (volume of the hip extensor muscle group, TFL, sartorius and gluteus maximus) indicating a more targeted development may be needed for elite performance. Moreover, the need for targeted hypertrophy even within muscle groups is emphasised by the individual muscle findings with three muscles being larger in elite vs. sub-elite sprinters in both absolute and relative terms (TFL, absolute +57%, relative +37%; sartorius, absolute, +47%, relative +28%; gluteus maximus, absolute +45%, relative +25%) with the gluteus maximus alone explaining 33.6% (relative volume) to 43.8% (absolute volume) of the variance in performance amongst sprinters. However, our knowledge of the exercises needed to facilitate hypertrophy of these individual muscles (TFL, sartorius, gluteus maximus) is relatively limited. It is also possible given the greater sprint training experience of the elite group in this study that regular, prolonged sprint training may stimulate many of the morphological characteristics we have observed (40).

Conclusion

In conclusion this investigation highlights for the first time the importance of highly inhomogeneous muscularity, with a specific pattern of distribution for elite sprint running performance compared to sub-elite sprinters and controls. Specifically, this experiment revealed for the first time that the hip extensors of elite sprinters were of a greater absolute and relative size and both these measurements were related to performance, such that hip extensor absolute volume explained 47.5% of the variability in sprint running performance. Individual muscles showed particularly pronounced differences in the muscle distribution of elite sprinters, with three hip muscles (TFL, sartorius and gluteus maximus) consistently larger in absolute and relative terms, and the absolute volume of the gluteus maximus alone

630 explained 43.8% of the variance in sprint performance. Based on this novel evidence it is
631 therefore recommended that coaches and athletes be attentive to the development of muscle
632 volume in these specific lower body muscles to enhance sprint running performance.

633 *Acknowledgements*

634 This investigation was financially supported by UK Athletics and the UK Strength and
635 Conditioning Association. The authors would like to thank the participants who gave up their
636 time to take part in this research study, Dr. Bill Haug for his help with data analysis, and Mr.
637 Sam Power for his significant contribution and support in data acquisition.

638

639 *Conflicts of Interest*

640 No conflicts of interest are relevant to this article. The present results do not constitute
641 endorsement by the American College of Sports Medicine, and the authors declare that the
642 results of the study are presented clearly, honestly and without fabrication, falsification, or
643 inappropriate data manipulation.

644 REFERENCES

- 645 1. Čoh M, Hébert-Losier K, Štuhec S, Babić V, Supej M. Kinematics of Usain Bolt's
646 maximal sprint velocity. *Kinesiology*. 2018;50(2):172-80.
- 647 2. O'Brien TD, Reeves ND, Baltzopoulos V, Jones DA, Maganaris CN. Strong
648 relationships exist between muscle volume, joint power and whole-body external
649 mechanical power in adults and children. *Exp. Physiol.* 2009;94(6):731-8.
- 650 3. Cruz-Jentoft AJ, Bahat G, Bauer J et al. Sarcopenia: revised European consensus on
651 definition and diagnosis. *Age Ageing*. 2019;48(1):16-31.
- 652 4. Ema R, Sakaguchi M, Kawakami Y. Thigh and Psoas Major Muscularity and Its
653 Relation to Running Mechanics in Sprinters. *Med. Sci. Sports Exerc.* 2018:2085-91.
- 654 5. Handsfield GG, Knaus KR, Fiorentino NM, Meyer CH, Hart JM, Blemker SS.
655 Adding muscle where you need it: non-uniform hypertrophy patterns in elite sprinters.
656 *Scand. J. Med. Sci. Sports*. 2016:1-11.
- 657 6. Copaver K, Hertogh C, Hue O. The effects of psoas major and lumbar lordosis on hip
658 flexion and sprint performance. *Res. Q. Exerc. Sport*. 2012;83(2):160-7.
- 659 7. Sugisaki N, Kobayashi K, Tsuchie H, Kanehisa H. Associations Between Individual
660 Lower Limb Muscle Volumes and 100-m Sprint Time in Male Sprinters. *Int. J. Sports*
661 *Physiol. Perform.* 2017:1-19.
- 662 8. Tottori N, Suga T, Miyake Y et al. Hip Flexor and Knee Extensor Muscularity Are
663 Associated With Sprint Performance in Sprint-Trained Preadolescent Boys. *Pediatr.*
664 *Exerc. Sci.* 2018;30(1):115-23.
- 665 9. Sugisaki N, Kanehisa H, Tauchi K, Okazaki S, Iso S, Okada J. The Relationship
666 between 30-m Sprint Running Time and Muscle Cross-sectional Areas of the Psoas
667 Major and Lower Limb Muscles in Male College Short and Middle Distance Runners.
668 *Int J Sports Health Sci*. 2011;9:1-7.

- 669 10. Hoshikawa Y, Muramatsu M, Iida T et al. Influence of the psoas major and thigh
670 muscularity on 100-m times in junior sprinters. *Med. Sci. Sports Exerc.*
671 2006;38(12):2138-43.
- 672 11. Bex T, Iannaccone F, Stautemas J et al. Discriminant musculo-skeletal leg
673 characteristics between sprint and endurance elite Caucasian runners. *Scand. J. Med.*
674 *Sci. Sports.* 2017;27(3):275-81.
- 675 12. Chelly MS, Cherif N, Amar MB et al. Relationships of Peak Leg Power, 1 Maximal
676 Repetition Half Back Squat, and Leg Muscle Volume to 5-m Sprint Performance of
677 Junior Soccer Players. *J. Strength Cond. Res.* 2010;24(1):266-71.
- 678 13. Wang R, Hoffman JR, Tanigawa S et al. Isometric Mid-Thigh Pull Correlates with
679 Strength, Sprint and Agility Performance in Collegiate Rugby Union Players. *J.*
680 *Strength Cond. Res.* 2016;30(11):3051-6.
- 681 14. Blazeovich AJ, Jenkins DG. Predicting Sprint Running Times from Isokinetic and
682 Squat Lift Tests: A Regression Analysis. *J. Strength Cond. Res.* 1998;12(2):101-3.
- 683 15. UK Athletics 2018 Selection Policies. [Internet]. Available from:
684 <https://www.uka.org.uk/performance/2018-selection-policies/>.
- 685 16. Janczewska L, Lebedziński B, Stupnicki R, Biernat E. Assessment of physical
686 activity by applying IPAQ questionnaire. *Phys Educ Sport.* 2008;52(-1):46-52.
- 687 17. Eston R, Hawes M, Martin AD, Reilly T. *Kinanthropometry and Exercise Physiology*
688 *Labratory Manual Volume 1: Anthropometry.* 3rd ed.: Routledge; 2009. p. 4-53.
- 689 18. Durnin JVGA, Womersley J. Body fat assessed from total body density and its
690 estimation from skinfold thickness: measurements on 481 men and women aged from
691 16 to 72 Years. *Br. J. Nutr.* 2007;32(01):77-97.
- 692 19. Siri WE. The gross composition of the body. In: CA Tobias, JH Lawrence editors.
693 *Advances in Biol and Med Phys.* New York: Academic Press; 1956, pp. 239-80.

- 694 20. Benjamini Y, Hochberg Y. Controlling the False Discovery Rate: A Practical and
695 Powerful Approach to Multiple Testing. *J R Stat Soc Series B Stat Methodol.*
696 1995;57(1):289-300.
- 697 21. Evangelidis PE, Massey GJ, Pain MT, Folland JP. Strength and size relationships of
698 the quadriceps and hamstrings with special reference to reciprocal muscle balance.
699 *Eur. J. Appl. Physiol.* 2016;116(3):593-600.
- 700 22. Massey GJ, Balshaw TG, Maden-Wilkinson TM, Tillin NA, Folland JP. Tendinous
701 Tissue Adaptation to Explosive- vs. Sustained-Contraction Strength Training. *Front.*
702 *Physiol.* 2018;9:1170.
- 703 23. Handsfield GG, Meyer CH, Hart JM, Abel MF, Blemker SS. Relationships of 35
704 lower limb muscles to height and body mass quantified using MRI. *J. Biomech.*
705 2014;47(3):631-8.
- 706 24. Dorn TW, Schache AG, Pandy MG. Muscular strategy shift in human running:
707 dependence of running speed on hip and ankle muscle performance. *J. Exp. Biol.*
708 2012;215(Pt 11):1944-56.
- 709 25. Wiemann K, Tidow G. Relative activity of hip and knee extensors in sprinting -
710 implications for training. *New Stud Ath.* 1995;10:29-49.
- 711 26. Morin JB, Gimenez P, Edouard P et al. Sprint Acceleration Mechanics: The Major
712 Role of Hamstrings in Horizontal Force Production. *Front. Physiol.* 2015;6:404.
- 713 27. Delecluse C. Influence of Strength Training on Sprint Running Performance. Current
714 Findings and Implications for Training. *Sports Med.* 1997;24(3):147-56.
- 715 28. Schache AG, Blanch PD, Dorn TW, Brown NAT, Rosemond D, Pandy MG. Effect of
716 running speed on lower-limb joint kinetics. *Med. Sci. Sports Exerc.* 2011;43(7):1260-
717 71.

- 718 29. Majumdar AS, Robergs RA. The Science of Speed: Determinants of Performance in
719 the 100 m Sprint. *Int J Sports Sci Coa*. 2011;6(3):479-93.
- 720 30. Morin JB, Edouard P, Samozino P. New Insights into Sprint Biomechanics and
721 Determinants of Elite 100m Performance. *New Stud Ath*. 2013;3(4):87-103.
- 722 31. Weyand PG, Davis JA. Running performance has a structural basis. *J. Exp. Biol*.
723 2005;208(Pt 14):2625-31.
- 724 32. Andersson EA, Nilsson J, Thorstensson A. Intramuscular EMG from the hip flexor
725 muscles during human locomotion. *Acta Physiol. Scand*. 1997;161:361-70.
- 726 33. Evangelidis PE, Massey GJ, Ferguson RA, Wheeler PC, Pain MTG, Folland JP. The
727 functional significance of hamstrings composition: is it really a "fast" muscle group?
728 *Scand. J. Med. Sci. Sports*. 2017;27(11):1181-9.
- 729 34. Schache AG, Dorn TW, Williams GP, Brown NA, Pandy MG. Lower-limb muscular
730 strategies for increasing running speed. *J. Orthop. Sports Phys. Ther*.
731 2014;44(10):813-24.
- 732 35. Belli A, Kyröläinen H, Komi PV. Moment and Power of Lower Limb Joints in
733 Running. *Int. J. Sports Med*. 2002;23:136-41.
- 734 36. Wilson GJ, Murphy AJ. The Use of Isometric Tests of Muscular Function in Athletic
735 Assessment. *Sports Med*. 1996;22(1):19-37.
- 736 37. Newman MA, Tarpenning KM, Marino FE. Relationships Between Isokinetic Knee
737 Strength, Single-Sprint Performance, and Repeated-Sprint Ability in Football Players.
738 *J. Strength Cond. Res*. 2004;18(4):867-72.
- 739 38. Cronin JB, Hansen KT. Strength and Power Predictors of Sports Speed. *J. Strength*
740 *Cond. Res*. 2005;19(2):349-57.

- 741 39. Baker D, Wilson G, Carlyon R. Generality versus specificity: a comparison of
742 dynamic and isometric measures of strength and speed-strength. *Eur. J. Appl. Physiol.*
743 1994;68:350-5.
- 744 40. Nuell S, Illera-Dominguez VR, Carmona G et al. Hypertrophic muscle changes and
745 sprint performance enhancement during a sprint-based training macrocycle in
746 national-level sprinters. *Eur J Sport Sci.* 2019:1-10.
- 747

Table 1. Performance and training status, and anthropometric characteristics of elite sprinters (n=5), sub-elite sprinters (n=26) and untrained controls (n=11). Data are presented as mean \pm SD.

	Controls	Sub-Elite Sprinters		Elite Sprinters	
	Mean \pm SD	Mean \pm SD	Range	Mean \pm SD	Range
Performance & Training Status					
SBE ₁₀₀ (s)	-	10.80 \pm 0.30	10.36-11.50	10.10 \pm 0.07 **	10.03-10.21
PBE ₁₀₀ (s)	-	10.69 \pm 0.26	10.34-11.25	9.99 \pm 0.07 **	9.91-10.08
Sprint Training Duration (Yrs)	-	5.3 \pm 2.6		9.2 \pm 3.4 **	
Resistance Training Duration (Yrs)	-	3.5 \pm 2.0		8.1 \pm 2.6 **	
Activity Level (MET-min.week ⁻¹)	2006 \pm 825				
Anthropometrics					
Age (yrs)	25.8 \pm 2.6	22.0 \pm 2.2 ††		27.4 \pm 4.1 **	
Height (m)	1.80 \pm 0.08	1.78 \pm 0.06		1.83 \pm 0.06	
Body Mass (kg)	75.2 \pm 5.6	75.4 \pm 7.3		86.4 \pm 6.7 **,†	
Body Mass Index (kg.m ⁻²)	23.3 \pm 1.8	24.3 \pm 2.4		25.0 \pm 1.0	
Sum of 8 Skinfold (mm)	88 \pm 32	53 \pm 14 ††		39 \pm 4 ††	
Body Fat Percentage (%)	15.5 \pm 4.3	11.2 \pm 3.1 ††		8.3 \pm 1.2 ††	
Fat Free Mass (kg)	63.5 \pm 4.7	67.0 \pm 6.7		79.8 \pm 6.1 **,††	
Waist:Glute Ratio (-)	0.81 \pm 0.02	0.82 \pm 0.04		0.84 \pm 0.05	

Significantly different to sub-elite: * P \leq 0.05 and ** P \leq 0.01, Significantly different to controls: † P \leq 0.05 and †† P \leq 0.01.

Table 2. Absolute and relative muscle volume of all muscles, five functional muscle groups and 23 individual muscles / compartments of elite sprinters (n=5), sub-elite sprinters (n=26) and untrained controls (n=11). Number of axial images / slices used to assess the volume of each muscle were averaged across all participants. Muscle volume data are presented as group mean \pm SD, with individual measurements the average of both sides/legs (i.e. unilateral).

Muscle Group / Muscle or Compartment	No. of Slices	Absolute Muscle Volume (cm ³)			Relative Muscle Volume (cm ³ .kg ⁻¹)		
		Control Group	Sub-Elite Sprinters	Elite Sprinters	Control Group	Sub-Elite Sprinters	Elite Sprinters
All Muscles		7628 \pm 1548	9164 \pm 1207 ^{††}	11323 \pm 1328 ^{**,††}	101.42 \pm 7.55	121.51 \pm 10.05 ^{††}	131.26 \pm 6.76 ^{††}
Hip Flexors		1031 \pm 151	1314 \pm 216 ^{††}	1620 \pm 200 ^{**,††}	13.75 \pm 2.16	17.42 \pm 2.27 ^{††}	18.82 \pm 1.83 ^{††}
Hip Extensors		2257 \pm 220	3029 \pm 422 ^{††}	4002 \pm 489 ^{**,††}	30.10 \pm 3.14	40.16 \pm 3.77 ^{††}	46.39 \pm 2.88 ^{**,††}
Knee Flexors		1460 \pm 196	1859 \pm 301 ^{††}	2304 \pm 178 ^{**,††}	19.45 \pm 2.72	24.61 \pm 2.79 ^{††}	26.78 \pm 0.76 ^{††}
Knee Extensors		2202 \pm 315	2636 \pm 401 ^{††}	3218 \pm 400 ^{**,††}	29.21 \pm 3.09	35.00 \pm 4.36 ^{††}	37.31 \pm 2.48 ^{††}
Plantarflexors		860 \pm 172	943 \pm 156	1112 \pm 181 [†]	11.39 \pm 1.92	12.48 \pm 1.40	12.92 \pm 1.78
Iliopsoas	18	514 \pm 75	618 \pm 101 [†]	702 \pm 97 ^{††}	6.84 \pm 1.03	8.18 \pm 0.97 ^{††}	8.18 \pm 1.10
Sartorius	28	142 \pm 25	209 \pm 50 ^{††}	306 \pm 46 ^{**,††}	1.89 \pm 0.28	2.77 \pm 0.62 ^{††}	3.56 \pm 0.40 ^{*,††}
Tensor Fasciae Latae	15	73 \pm 24	86 \pm 25	135 \pm 41 ^{**,††}	0.97 \pm 0.36	1.14 \pm 0.29	1.56 \pm 0.39 ^{*,††}
Adductor Magnus	16	624 \pm 81	828 \pm 128 ^{††}	1056 \pm 83 ^{**,††}	8.30 \pm 0.88	10.99 \pm 1.46 ^{††}	12.31 \pm 1.05 ^{††}
Gracilis	17	98 \pm 23	142 \pm 37 ^{††}	180 \pm 37 ^{††}	1.31 \pm 0.30	1.89 \pm 0.45 ^{††}	2.10 \pm 0.39 ^{††}
Gluteus Maximus	16	931 \pm 108	1257 \pm 197 ^{††}	1797 \pm 376 ^{**,††}	12.40 \pm 1.39	16.65 \pm 1.82 ^{††}	20.75 \pm 3.15 ^{**,††}
Gluteus Medius	10	384 \pm 49	405 \pm 69	434 \pm 92	5.11 \pm 0.51	5.38 \pm 0.75	5.01 \pm 0.75
Gluteus Minimus	9	199 \pm 39	170 \pm 36	192 \pm 46	2.66 \pm 0.58	2.25 \pm 0.44	2.22 \pm 0.48
Rectus Femoris	21	303 \pm 55	401 \pm 78 ^{††}	476 \pm 45 ^{††}	4.05 \pm 0.81	5.33 \pm 0.98 ^{††}	5.53 \pm 0.38 [†]

Vastus Lateralis	22	743 ± 98	925 ± 156 ^{††}	1132 ± 180 [†]	9.88 ± 1.20	12.26 ± 1.65 ^{††}	13.07 ± 1.09 ^{††}
Vastus Intermedius	23	680 ± 115	789 ± 140	962 ± 145 ^{*,††}	9.01 ± 1.20	10.48 ± 1.63 [†]	11.17 ± 1.33 [†]
Vastus Medialis	19	476 ± 111	521 ± 79	649 ± 97 ^{*,††}	6.28 ± 1.11	6.92 ± 0.89	7.53 ± 0.89
Semimembranosus	17	262 ± 18	327 ± 59 ^{††}	359 ± 60 ^{††}	3.50 ± 0.33	4.34 ± 0.63 ^{††}	4.16 ± 0.56
Semitendinosus	15	219 ± 39	350 ± 79 ^{††}	449 ± 70 ^{*,††}	2.93 ± 0.64	4.63 ± 0.86 ^{††}	5.20 ± 0.54 ^{††}
Biceps Femoris Long Head	18	221 ± 42	267 ± 47 [†]	340 ± 31 ^{**,††}	2.97 ± 0.71	3.55 ± 0.54 [†]	3.96 ± 0.32 ^{††}
Biceps Femoris Short Head	7	110 ± 28	131 ± 34	167 ± 26 ^{††}	1.46 ± 0.36	1.73 ± 0.39	1.94 ± 0.29
Popliteus	16	19 ± 6	17 ± 5	23 ± 5	0.26 ± 0.06	0.22 ± 0.07	0.27 ± 0.05
Lateral Gastrocnemius	13	156 ± 41	170 ± 37	202 ± 34	2.06 ± 0.47	2.25 ± 0.38	2.36 ± 0.51
Medial Gastrocnemius	14	251 ± 52	262 ± 58	300 ± 38	3.33 ± 0.62	3.50 ± 0.42	3.50 ± 0.42
Soleus	22	453 ± 95	510 ± 76	610 ± 137 ^{††}	6.00 ± 1.08	6.77 ± 0.76	7.05 ± 1.25
Anterior Compartment	20	291 ± 47	273 ± 47	302 ± 59	3.87 ± 0.53	3.62 ± 0.52	3.48 ± 0.46
Lateral Compartment	21	153 ± 35	161 ± 42	147 ± 32	2.02 ± 0.39	2.13 ± 0.46	1.69 ± 0.27
Posterior Compartment	20	326 ± 93	345 ± 71	401 ± 76	4.32 ± 1.12	4.57 ± 0.82	4.63 ± 0.60

Significantly different to sub-elite: * P≤0.05 and ** P≤0.01, Significantly different to controls: [†] P≤0.05 and ^{††} P≤0.01.

All muscles is the sum of muscle volumes from all the muscles/compartments listed.

Table 3. Pearson's product moment correlation coefficients between Seasons Best Equivalent 100 m (SBE₁₀₀) and absolute and relative muscle volume of all muscles, five functional muscle groups and 23 individual muscles in the whole cohort of sprinters (n=31).

Muscle Group / Muscle	Absolute Muscle Volume (cm ³)	Relative Muscle Volume (cm ³ .kg ⁻¹)
All Muscles	-0.629**	-0.422*
Hip Flexors	-0.563 **	-0.299
Hip Extensors	-0.689 ***	-0.560 **
Knee Flexors	-0.682 ***	-0.522 **
Knee Extensors	-0.495 **	-0.178
Plantarflexors	-0.537 **	-0.309
Iliopsoas	-0.442 *	-0.120
Sartorius	-0.639 ***	-0.484
Tensor Fasciae Latae	-0.547 **	-0.454
Adductor Magnus	-0.582 **	-0.289
Gracilis	-0.564 **	-0.377
Gluteus Maximus	-0.662 ***	-0.580 *
Gluteus Medius	-0.227	0.152
Gluteus Minimus	-0.254	0.040
Rectus Femoris	-0.409 *	-0.090
Vastus Lateralis	-0.475 *	-0.199
Vastus Intermedius	-0.443 *	-0.154
Vastus Medialis	-0.431 *	-0.114
Semimembranosus	-0.478 *	-0.194
Semitendinosus	-0.530 **	-0.342
Biceps Femoris Long Head	-0.475 *	-0.190
Biceps Femoris Short Head	-0.511 *	-0.341
Popliteus	-0.435 *	-0.260
Lateral Gastrocnemius	-0.578 **	-0.398
Medial Gastrocnemius	-0.437 *	-0.230
Soleus	-0.474 *	-0.196
Anterior Compartment	-0.272	0.092
Lateral Compartment	-0.192	0.045
Posterior Compartment	-0.290	0.014

Significant correlations: * $P \leq 0.05$; ** $P \leq 0.01$; and *** $P \leq 0.001$ following correction for multiple comparisons.

4 **FIGURE CAPTIONS**

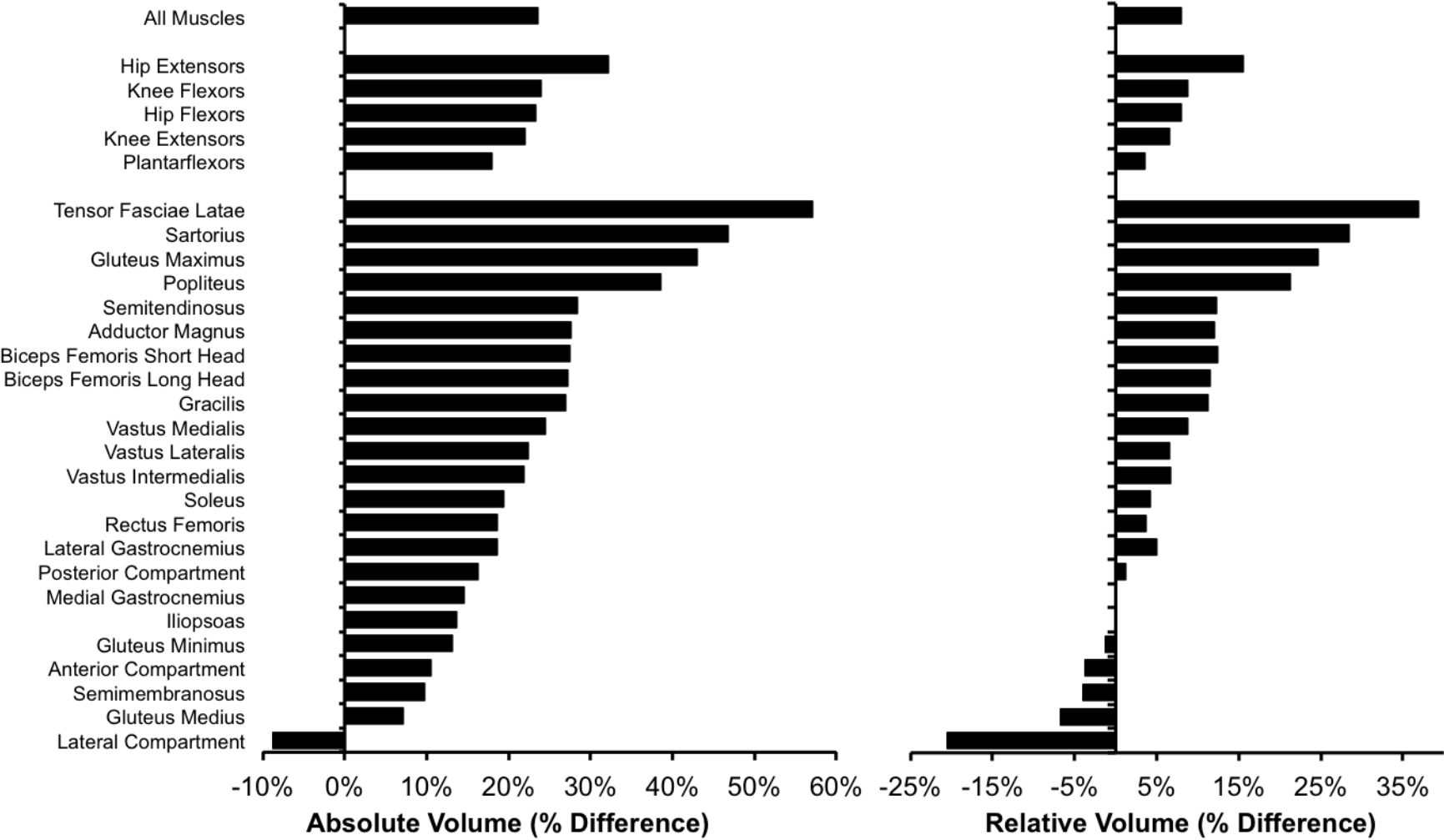
5 **Figure 1.** Percentage differences in absolute and relative muscle volumes of all muscles, five
6 functional muscle groups and 23 muscles / compartments between elite (n=5) vs. sub-elite
7 (n=26) sprinters. A positive value indicates greater volume of elite sprinters. The functional
8 muscle groups and individual muscles are ordered according to the magnitude of the
9 percentage differences for absolute muscle volume.

10

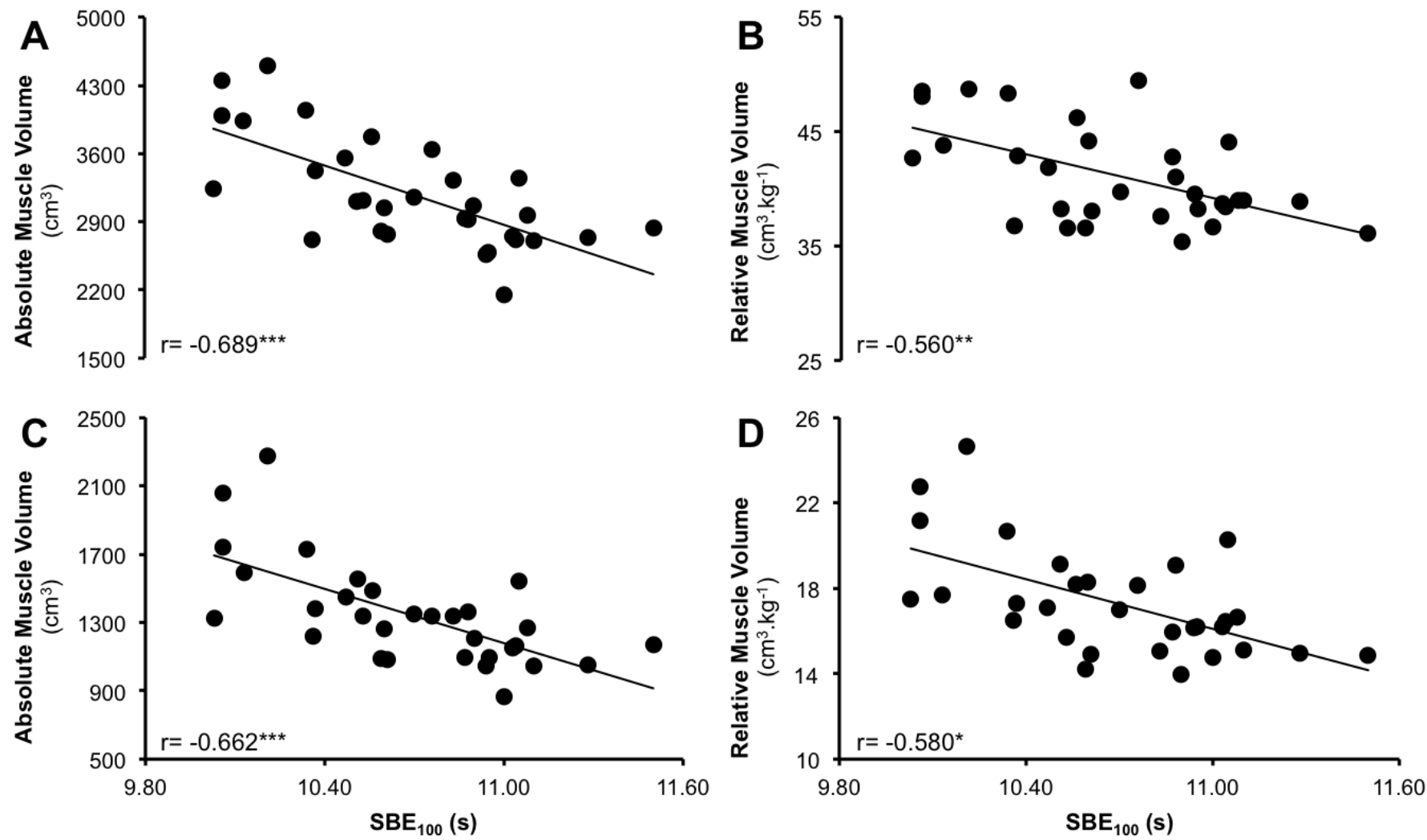
11 **Figure 2.** The relationships between Seasons Best Equivalent 100 m (SBE₁₀₀) and (A)
12 Absolute hip extensor volume; (B) Relative hip extensor volume; (C) Absolute gluteus
13 maximus volume; (D) Relative gluteus maximus volume. Significant correlations: * $P \leq 0.05$;
14 ** $P \leq 0.01$; and *** $P \leq 0.001$ following correction for multiple comparisons.

15

16 **Figure 3.** Comparison of absolute and relative isometric maximum voluntary torque of 5
17 functional muscle groups between elite (n=5) vs sub-elite (n=26) sprinters vs untrained
18 controls (n=11). Data are presented as group mean \pm SD, with individual measurements the
19 average of both legs. Significantly different to controls: * $P \leq 0.05$ and ** $P \leq 0.01$.

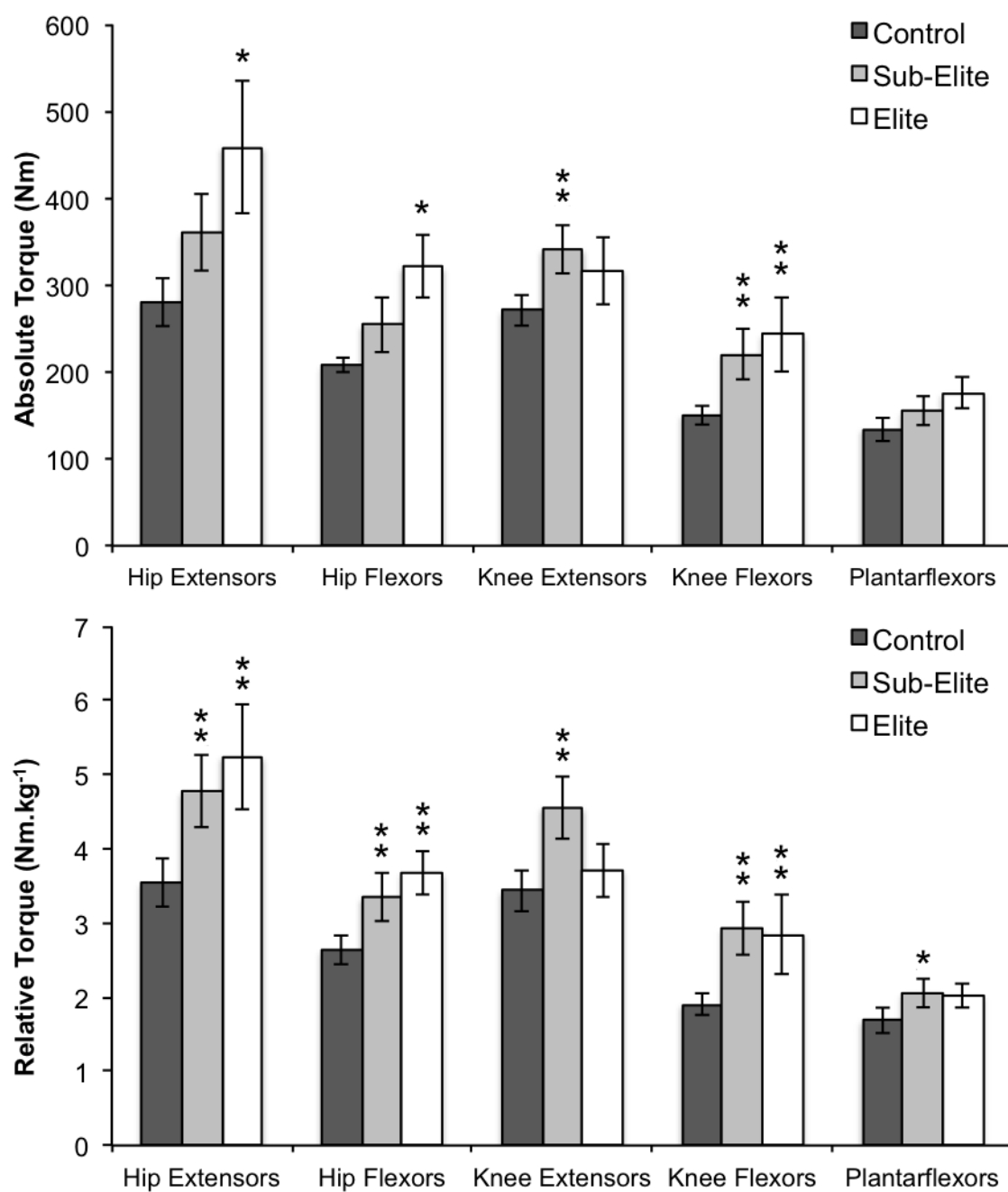


23 [Fig. 2]
24



25

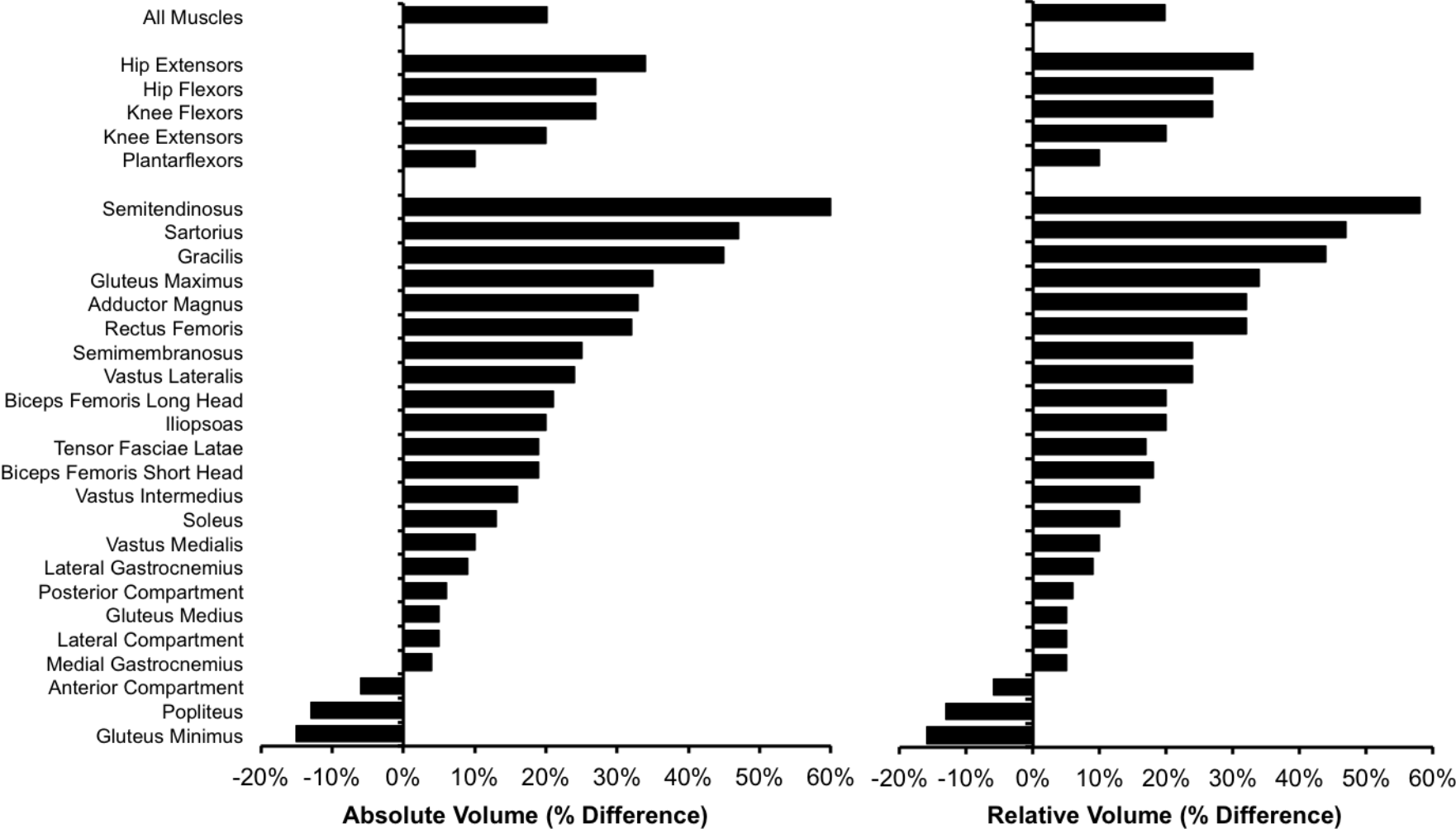
[Fig. 3]



SUPPLEMENTAL DIGITAL CONTENT

Supplemental Digital Content 1. Percentage differences in absolute and relative muscle volumes of all muscles, five functional muscle groups and 23 muscles / compartments between sub-elite sprinters (n=26) vs. controls (n=11). A positive value indicates greater volume of sub-elite sprinters. The functional muscle groups and individual muscles are ordered according to the magnitude of the percentage differences for absolute muscle volume. TIFF

Supplemental Digital Content 2. A summary table of the observed significant differences between sub-elite sprinters vs. controls, and elite sprinters vs. sub-elite sprinters. Docx



Supplemental Digital Content 2. A summary table of the observed significant differences between sub-elite sprinters vs. controls, and elite sprinters vs. sub-elite sprinters.

	Sub-Elite Sprinters (n=26)	Elite Sprinters (n=5)
	vs.	vs.
	Controls (n=11)	Sub-Elite Sprinters (n=26)
Absolute Muscle Volume (cm³)		
Total Volume	+20%	+24%
Functional Muscle Groups	4/5 muscle groups (+20-34%; not PF)	4/5 muscle groups (+22-32%; not PF)
Individual Muscles	10 muscles (+21-60%)	8 muscles (+22-57%)
Relative Muscle Volume (cm³.kg⁻¹)		
Total Volume	+20%	-
Functional Muscle Groups	4/5 muscle groups (+20-33%; not PF)	1/5 muscle groups (+15% HE)
Individual Muscles	12 muscles (+16-58%)	3 muscles (+25-37%)

PF, plantarflexors; HE, hip extensors. All listed differences were significant with $P \leq 0.05$.