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Author

Bellinger, Phillip, Bourne, Matthew, Duhig, Steven, Lievens, Eline, Kennedy, Ben, Martin, Andrew, Cooper, Christopher, Tredrea, Matthew, Rice, Hal, Derave, Wim, Minahan, Clare

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1 **Relationships between lower limb muscle characteristics and force-velocity profiles**
2 **derived during sprinting and jumping**

3 PHILLIP BELLINGER^{1,2}, MATTHEW BOURNE^{1,3}, STEVEN DUHIG^{1,3}, ELINE
4 LIEVENS⁴, BEN KENNEDY⁶, ANDREW MARTIN¹, CHRISTOPHER COOPER¹,
5 MATTHEW TREDREA⁵, HAL RICE⁶, WIM DERAVE⁴ and CLARE MINAHAN¹

6 ¹Griffith Sports Science, Griffith University, Gold Coast, Australia

7 ²Queensland Academy of Sport, Queensland, Australia

8 ³Gold Coast Centre for Orthopaedics Research, Engineering and Education (GCORE),
9 Menzies Health Institute Queensland, Griffith University, Australia

10 ⁴Department of Movement and Sports Sciences, Ghent University, Ghent, Belgium

11 ⁵Department of Rehabilitation, Nutrition and Sport, La Trobe University College of Science
12 Health and Engineering, Nutrition and Sport, Bundoora, Australia

13 ⁶Qscan Radiology, Australia.

14 **Correspondence:**

15 Phillip Bellinger

16 School of Allied Health Sciences, Griffith University, Queensland, Australia, 4222.

17 Phone: (617) 5552 9219 Fax: (617) 5552 8674 Email: p.bellinger@griffith.edu.au

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22

23 **ABSTRACT**

24 **Purpose:** To identify the relationships between lower limb muscle characteristics and the
25 mechanical variables derived from the vertical (jumping) and horizontal (sprinting) force-
26 velocity-power (FVP) profiles. **Methods:** Nineteen sub-elite male rugby league players
27 performed a series of squat jumps and linear 30 m sprints to derive the vertical and horizontal
28 FVP profiles, respectively. The theoretical maximal force ($F0$), velocity ($V0$) and power
29 ($Pmax$) were derived from both the vertical (i.e., $vF0$, $vV0$ and $vPmax$) and horizontal (i.e.,
30 $hF0$, $hV0$ and $hPmax$) FVP profiles. Vastus lateralis (VL), biceps femoris (BF) long head and
31 gastrocnemius medialis (GM) and lateralis muscle fascicle length, pennation angle and
32 thickness were measured using B-mode ultrasonography. Magnetic resonance (MR) imaging
33 was used to calculate volumes of major lower limb muscles, while proton MR spectroscopy
34 was used to quantify the carnosine content of the GM to estimate muscle fiber typology.
35 **Results:** Variation in $vPmax$ was best explained by GM muscle fiber typology (i.e., greater
36 estimated proportion of type II fibers) and VL volume (adjusted $r^2=0.440$; $P=0.006$), while
37 adductor and vastus medialis volume and GM muscle fiber typology explained the most
38 variation in $hPmax$ (adjusted $r^2=0.634$, $P=0.032$). Rectus femoris and VL volume explained
39 variation in $vF0$ ($r^2=0.430$; $P=0.008$), while adductor and vastus medialis volume explained
40 variation in $hF0$ ($r^2=0.432$; $P=0.007$). Variation in $vV0$ and $hV0$ were best explained by GM
41 muscle fiber typology (adjusted $r^2=0.580$, $P<0.001$) and GM muscle fiber typology and BF
42 short head volume (adjusted $r^2 = 0.590$, $P<0.001$), respectively. **Conclusion:** Muscle fiber
43 typology and muscle volume are strong determinants of maximal muscle power in jumping and
44 sprinting by influencing the velocity- and force-orientated mechanical variables.

45 **Keywords:** MUSCLE FIBER TYPE COMPOSITION; MUSCLE FASCICLE LENGTH;
46 MUSCLE VOLUME; CARNOSINE; JUMP PERFORMANCE; SPRINT PERFORMANCE

47 INTRODUCTION

48 Generating a large amount of force at a high contraction (or movement) velocity is critical for
49 many ‘explosive’ movements and is a key performance variable in many sports (1). Indeed, for
50 the sport of rugby league, lower limb maximal muscle power is one of the strongest
51 discriminatory performance variables that differentiates between elite National Rugby League
52 (NRL) players and their second-division counterparts (2). Given that maximal muscle power
53 is directly influenced by the underlying force and velocity mechanical outputs, the force–
54 velocity (FV) and power–velocity (PV) relationships have been used to profile the theoretical
55 maximal mechanical output during sprinting and jumping activities (3, 4). The assessment of
56 the FV and PV relationships during these movements characterizes the external force
57 production capabilities of the lower limbs by identifying the theoretical maximum force ($F0$),
58 velocity ($V0$) and power ($Pmax$) produced during sprinting (i.e., horizontal; $hF0$, $hV0$ and
59 $hPmax$) or jumping (i.e., vertical; $vF0$, $vV0$ and $vPmax$) (3, 5). While these mechanical
60 capabilities are clearly important for sprinting and jumping performance, the lower limb muscle
61 characteristics underpinning these mechanical capabilities are yet to be fully elucidated.

62 The external force production capabilities of the lower limbs are likely to be influenced by
63 several muscle characteristics, including muscle architecture (i.e., fascicle length, pennation
64 angle and thickness), morphology (i.e., muscle volume) and the distribution of type I and II
65 muscle fibers (i.e., fiber typology). Muscle fiber typology is largely dependent on genetic
66 predisposition and transition between type I and II fibers is not thought to occur very readily
67 in response to training (6). In contrast, muscle volume and architecture are more malleable to
68 training and changes in these characteristics can occur quite rapidly (7). While inter-individual
69 differences in the FV profile have previously been utilized to individualize training prescription
70 (8), a better understanding of the muscle characteristics that modulate this profile may improve
71 our ability to prescribe performance enhancing exercise interventions. For example, identifying

72 the extent to which muscle architecture and volume contribute to the external force production
73 capabilities may inform the design of training interventions that preferentially target
74 adaptations in these characteristics, thus maximising the training response. Furthermore,
75 greater insight into how muscle fiber typology contributes to the external force production
76 capabilities of the lower limbs may influence the interpretation of the FV profile for the purpose
77 of individualizing training programs (8). Interestingly, in high level athletes there are trivial to
78 small correlations between the maximal mechanical variables derived from vertical and
79 horizontal FV and PV profiles (9). That is, an athlete who can produce a large vFO does not
80 necessarily have the capacity to produce an equally high hFO . Although this divergence might
81 be partly explained by differences in force orientation ability between sprinting and jumping,
82 it also suggests that the muscular characteristics underpinning the mechanical variables derived
83 from horizontal and vertical FV and PV profiles are likely to differ significantly.

84 While few studies have determined the muscular characteristics that underpin the maximal
85 mechanical parameters of the vertical and horizontal FV and PV profiles, the associations
86 between muscle characteristics and performance metrics (i.e., sprint times or jump height)
87 and/or levels of performance (i.e., trained and untrained) have been reported (10-18). For
88 example, previous research has reported a significant correlation ($r = -0.69$) between the
89 proportion of type II muscle fibers and 100-m sprint time (15) and squat jump mean mechanical
90 power (19), suggesting that muscle fiber typology may influence the external force production
91 capabilities of the lower limbs. Muscle architecture may also influence the FV and PV
92 mechanical parameters given that muscles with longer fascicles possess a greater shortening
93 velocity (20). Furthermore, elite 100 m sprinters (10.0 – 10.9 s) display longer fascicles in the
94 vastus lateralis (VL), and the gastrocnemius medial (GM) and gastrocnemius lateralis (GL)
95 compared to their sub-elite counterparts (11.0 – 11.7 s) (14) and distance runners (10). Recent
96 work (21) reported that GM muscle fascicle length accounted for almost half of the difference

97 in plantarflexion $V0$ between young and old men, while quadriceps thickness and VL pennation
98 angle explained ~62% of the variation in countermovement jump $vF0$ (22). Given that an
99 increase in fiber pennation angle would result in an increase in the number of sarcomeres in
100 parallel, and presumably a larger physiological cross-sectional area, it could also be expected
101 that this would result in a larger force generating capacity (23).

102 Most hip- and knee-crossing muscles are significantly larger in sprinters and long jumpers
103 compared to recreationally active individuals (11, 18, 24) and endurance runners (12) and total
104 thigh muscle volume is associated with faster 5-m sprint times and greater squat jump power
105 output (13). It could be postulated that the longer ground contact times during the early phase
106 of sprint running, allows the time for higher levels of muscle force to be produced. Thus,
107 muscle characteristics, such as volume, that directly influence maximal muscle force are likely
108 to affect $F0$. Specifically, the adductors (ADD) provide a major contribution to hip extension
109 torque during the late-swing to early-contact phase of sprint acceleration (25), while knee
110 flexor and extensor torque is thought to contribute to the swing and stance phases during
111 sprinting (26). Despite these observations, the associations between lower limb muscle
112 characteristics and the maximal mechanical parameters that underpin sprint running and
113 jumping performance have not been studied.

114 The primary aim of the present study was to determine the influence that lower limb muscle
115 architecture, morphology, and fiber typology have on the maximal mechanical parameters of
116 the FV and PV profiles derived during sprinting and jumping in sub-elite rugby league players.
117 We hypothesized that; i) muscle fiber typology (greater estimated proportion of type II fibers)
118 would be positively associated with $vV0$, $hV0$, $vPmax$ and $hPmax$, ii) the fascicle length of
119 lower limb muscles would be associated with $hV0$ and $hPmax$ while the fascicle length of the
120 VL would be associated with $vV0$ and $vPmax$, iii) the volume of most hip and knee-crossing
121 muscles, but not ankle-crossing muscles, would be positively associated with $hF0$ and $hPmax$,

122 and; iv) the volume of knee extensor muscles, as well as the angle of pennation and muscle
123 thickness of the VL would be positively associated with vFO and $vPmax$.

124 **METHODOLOGY**

125 *Participants*

126 Nineteen male rugby-league players (sex: age: 19.2 ± 0.7 years; height 180.7 ± 5.6 cm; body
127 mass 89.9 ± 10.0 kg) participated in the current study. The players were from the same elite
128 youth development system within an Australian NRL club. All players were involved in full
129 training and competition and had no history of lower-limb injury within twelve months of
130 testing and had at least four years of experience in resistance training. All players provided
131 written informed consent prior to participating in this study, which was approved by the Griffith
132 University Human Research Ethics Committee.

133 *Study design*

134 Data collection was conducted during a 4-day testing period following the 2019 NRL
135 preseason. Participants had a week of reduced training load following the completion of the
136 preseason preparation period as the team had a bye in the first round of competition and the
137 testing was completed at the end of this week. Participants underwent magnetic resonance
138 (MR) imaging of their entire lower limb to determine volumes of the major hip, knee and ankle-
139 spanning muscles, and proton MR spectroscopy (1H -MRS) of the GM to estimate muscle fiber
140 typology (27). In addition, muscle architecture of the biceps femoris long head (BFLH), VL,
141 and GM and GL were assessed via two-dimensional (2D) ultrasound. Figure 1 displays an
142 overview of these measurements. Subsequently, each participant performed one session of
143 maximal squat jumps with additional loads of 10-100% of their body mass to determine the
144 mechanical parameters associated with the vertical FV profile. In a separate session 48 hrs

145 later, each participant performed maximal 30-m sprints to determine the mechanical parameters
146 associated with the horizontal FV profile using a validated biomechanical model (3).

147 *FV relationship during the squat jump*

148 Each participant completed a 20 min general warm-up consisting of jogging and joint mobility
149 exercises, which was followed by a specific warm-up comprising several trials of both
150 unloaded and loaded squat jumps. Participants performed maximal unloaded (without external
151 load) and loaded (external loads ranging from 10-100% body mass) squat jumps to determine
152 the individual FV and PV relationships (4). For each squat jump, participants were instructed
153 to stand up straight and still on the centre of a bilateral force plate (ForceDecks, Vald
154 Performance, Australia) with a dowel rod (unloaded trials) or barbell (loaded trial) placed upon
155 their upper trapezius. External loads were added in sequential order until jump height fell below
156 15 cm. All subjects performed squat jumps with at least a load of 60% body mass until jump
157 height fell below 15 cm. For each squat jump, participants were asked to flex their hips and
158 knees while keeping their spine neutral, reach the starting squat height (~90° knee angle) and
159 pause for a count of 2 s, before applying as much voluntary force into the ground as possible
160 and jumping for maximum height. Countermovement was forbidden, carefully checked and
161 confirmed by the force plate technology. Two valid trials were performed with each load with
162 a 4 min recovery between different loads and trials. The force plates had a sampling rate of
163 1000 Hz and commercially available ForceDecks software (Vald Performance, Australia) was
164 used to analyse all squat jumps. The mean force, power and velocity was extracted from each
165 loading condition during the concentric phase which was defined as the sample immediately
166 prior to a 20 N change above the measured mass until the timepoint at which total vertical force
167 fell under the threshold of 20 N below mass. The FV and PV relationships were constructed by
168 plotting mean force and mean velocity using linear regression, while mean power and mean
169 velocity were plotted using second-degree polynomial functions. vFO and vVO were then

170 identified from the FV relationship as the x- and y-intercepts, respectively, while vP_{max} was
171 determined as the apex of the PV relationship (28). In our laboratory, $vF0$, $vV0$ and vP_{max} have
172 coefficient of variation (CV) values of 3.8%, 5.4% and 6.8%.

173 *FV relationship during sprinting*

174 All sprint testing was completed on the same well-maintained natural grass surface, and all
175 participants wore studded training shoes and training attire. Each participant performed a 15-
176 min on-field dynamic warm-up protocol which closely reflected the warm-up used before field-
177 based training sessions. Participants performed two linear 30-m sprints and sprint times were
178 recorded by infrared timing gates (Smartspeed, Fusion Sport, Australia) with split times every
179 5 m. All starts commenced from a static position and the upper body of each participant was
180 positioned as close as possible to the inter-gate beam of the first timing gate which was placed
181 on the starting line. The timing gates at the start line and 5 m line were mounted on separate
182 tripods 1.00/1.20 m above the ground level, while the remaining gates were mounted 1.30/1.50
183 m above the ground level. Based on available correction factors (29), we added 0.5 s to all
184 sprint times to ensure that the start time initiation was likely to coincide with the first rise of
185 the force production onto the ground. We computed individual PV and FV profiles using the
186 validated biomechanical model proposed by Samozino et al. (3) which have been shown to
187 have high reliability (CV and standard errors of measurement <5%). In brief, we used the
188 changes in running velocity over time to compute the acceleration of each participant's centre
189 of mass in the antero-posterior direction and then used the aerodynamic friction of force and
190 each athlete's body mass and height to estimate the net horizontal ground reaction force. $hF0$
191 and $hV0$ were then identified from the FV relationship as the x- and y-intercepts, respectively,
192 and hP_{max} was determined as the apex of the PV relationship. We used the mean of the
193 mechanical variables calculated from each of the two sprints in order to reduce the typical error
194 associated with using a single sprint (29).

195 *Carnosine quantification via ¹H-MRS*

196 Muscle carnosine content was measured by ¹H-MRS in the GM of each participant's right limb
197 in order to estimate muscle fiber typology. We chose to estimate the muscle fiber typology of
198 the GM because; i) we can measure carnosine reliably in this muscle, ii) carnosine content in
199 the GM muscle has been positively correlated with the percentage area occupied by type II
200 muscle fibers (27), and; iii) the GM makes a substantial contribution to force and power
201 production during running and jumping (30, 31). This suggests that the fiber composition of
202 the GM may be meaningful in the context of sprinting and jumping. ¹H-MRS measurements
203 were performed on a 3-T whole body magnetic resonance imaging (MRI) scanner (Philips
204 Medical Systems Best, The Netherlands). Participants were lying in a supine position, while
205 their lower leg was fixed in a spherical knee-coil. All the spectra were acquired using single
206 voxel point-resolved spectroscopy with the following parameters; repetition time of 2000 ms,
207 echo time of ~40 ms, number of excitations was 128 (carnosine) and 16 (water), spectral
208 bandwidth was 2048 Hz, and an acquisition time of 4 min 16 s (carnosine) and 32 s
209 (water). The voxel size was 40 mm x 15 mm x 20 mm. Spectral data analysis was carried out
210 using jMRUI (version 6.0) with carnosine peaks fitted and expressed relative to the internal
211 water signal.

212 Carnosine content (mM) was calculated using following formula:

213
$$C_m = \frac{(CS)}{(H_2O_s)} \cdot \frac{(H_2O_{T1r})}{(CT_{1r})} \cdot \frac{(H_2O_{T2r})}{(CT_{2r})} \cdot H_2O_{\text{muscle}} \cdot H_2O_{\text{protons}} \quad [1]$$

214 where C_m is the carnosine concentration, C_s is the carnosine signal, H_2O_s is the water signal,
215 C_{T1r} , C_{T2r} , H_2O_{T1r} , H_2O_{T2r} are the relaxation correction factors for carnosine (earlier described
216 by Baguet et al. (27)) and water (earlier described by MacMillan et al. (32)), H_2O_{muscle} is the
217 concentration of water in muscle, which was deducted from the molar concentration of water

218 (55,000 mM) and the approximate water content of skeletal muscle tissue (0.7 L/kg wet weight
219 of tissue) and H_2O_{proton} is the number of protons in water. The CV for test-retest inter-day
220 carnosine measurements in our laboratory was 4.3% (n = 15 participants). In the present study,
221 the carnosine concentration was converted to a Z-score based on the normal distribution of our
222 reference population. The absolute value of Z-score represents the distance between the
223 individual value of a participant and the reference population mean value in units of the
224 standard deviation. The reference sample population consisted of 40 recreationally active male
225 subjects (age: 22.4 ± 2.1 years, height: 176.1 ± 17.2 cm, body mass: 81.2 ± 11.9 kg) who were
226 scanned in our laboratory in the past 12 months.

227 *2D ultrasound imaging*

228 Muscle architecture was measured *in vivo* using 2D B-mode ultrasonography (frequency,
229 7MHz; depth, 50 mm; field of view, 10 x 39 mm) (Echo Blaster 128 CEXT, Telemed Medical
230 Systems, Milan, Italy). Bilateral muscle assessments included the VL (50% distance between
231 greater trochanter and lateral femoral condyle) (14), BFLH (50% distance between ischial
232 tuberosity and popliteal fold in the line of action of the BF) (33), GL (30% proximal distance
233 between the lateral tibial condyle and the lateral malleolus in the midline of the muscle) and
234 GM (at the same distance as GL, transferred medially, from the midline of the muscle) (14).
235 All images were taken in the longitudinal axis with the participant laying prone for GM, GL
236 and BF measures, and supine for VL. Images were acquired after a period of at least 5 min of
237 inactivity. In order to capture images, the ultrasound transducer was placed perpendicular to
238 the surface of the skin, parallel with the presumed fascicle angle at the aforementioned sites.
239 The transducer was then moved accordingly so that both superficial and deep aponeuroses were
240 aligned in parallel on the viewing screen. Water soluble conductive gel was placed on the
241 transducer surface to enhance image quality while minimal pressure was placed on the skin
242 surface to ensure no muscle distortion and maintain image quality. Two images were captured

243 at each site bilaterally with the highest quality image of the two used for analyses. Image
244 analysis was completed offline using publicly available software (ImageJ 1.52n, National
245 Institutes of Health, Bethesda, MD, USA). Muscle thickness was determined as the average
246 distance between superficial and intermediate aponeuroses at the left and right extremity of
247 each image. Subsequently, two fascicles of interest were outlined in each image and the mean
248 angle between each fascicle and the deep aponeurosis was determined as the pennation angle.
249 Given that the entire fascicle was not always visible in the field of view, fascicle length was
250 estimated using a previously validated equation (34) (fascicle length = muscle thickness x [sin
251 (pennation angle)]⁻¹). Intraclass correlation (ICC) and CV were 0.99-1.00 and 2.5-3.0% for
252 muscle thickness, 0.96-0.97 and 4.4-5.5% for pennation angle, and 0.96-0.98 and 4.4-5.4% for
253 fascicle length. For each muscle architecture measure, we used the mean of the right and left
254 leg for all analyses given that there were no significant differences in individual muscles from
255 either limb.

256 *Muscle volume*

257 Axial T1-weighted 3-dimensional (3D) fast field echo (FFE) sequences were acquired using a
258 3-T MRI scanner (Philips Medical Systems) from the level of the iliac crest to the ankle
259 spanning both legs while the participant lay supine in the scanner. The images were acquired
260 in 5 stations with ~210 slices per station and 10 mm overlap between stations. Slice thickness
261 was 2.0 mm, inter-slice gap was 0.0 mm, repetition time was 4.1 ms, echo time 1 was 1.44
262 milliseconds, and echo time 2 was 2.6 ms. The cross-sectional area (CSA) of lower limb
263 muscles or muscle groups of both legs were determined at predefined lengths of 20, 30, 40, 50,
264 60, 70 and 80% of the total muscle length by manually tracing the margin of the respective
265 muscle in the relevant axial slices using image analysis software (Mimics, version 17;
266 Materialise). The analysed muscles were the gluteus maximus (GMAX), medius (GMED) and
267 minimus (GMIN), tensor fascia latae (TFL), sartorius, iliacus, gracilis, adductor magnus,

268 longus and brevis, rectus femoris (RF), VL, vastus intermedius (VI), vastus medialis (VM),
269 semimembranosus, semitendinosus, BFLH, BF short head (BFSH), soleus, GM and GL. The
270 identification of the borders between adductor magnus, longus and brevis was difficult;
271 therefore, these muscles were analysed as a muscle group and referred to as ADD. All
272 segmentations were performed by two members of the research team. Muscle volume was
273 calculated under the assumption that the muscle is an ideal cylinder whereby the known
274 distance between slices was multiplied by the sum of the CSA of the total number of traced
275 slices. This methodology (i.e., using 8 slices) has been shown to have high levels of agreement
276 (i.e., differences of <0.005%) with muscle volume calculations using 50 slices (35). In order
277 to reduce the effects of body size on muscle size differences, we normalized muscle volume by
278 height and the product of height and body mass (11). For each muscle volume, we used the
279 mean of the right and left leg for all analyses given that there were no significant differences
280 in the muscle volume of individual muscles from either limb. The inter-rater reliability of the
281 normalized muscle volume of the semitendinosus, semimembranosus, BFLH, BFSH, gracilis,
282 ADD, GMAX, GMED and GMIN was extremely good (mean ICC = 0.973, CV = 2.0%). We
283 expressed the sum of all individual muscle volumes as total muscle volume.

284 *Statistical analysis*

285 Values are expressed as mean \pm SD. We first performed univariable linear regression analyses
286 to identify the muscle characteristics that were significantly associated with the mechanical
287 variables of the vertical and horizontal FV and PV relationships which allowed us to test our
288 different hypotheses. Following this, we performed stepwise linear regression to identify the
289 best combination of muscle characteristics that explained the most variation in the mechanical
290 variables. In order to reduce the number of comparisons in the stepwise regression models, we
291 only included muscle characteristics in the analysis if a significant r value ($p < 0.05$) was

292 identified with the given mechanical variable from the univariable analyses. Statistical software
293 was used for analysis (SPSS 26.0 for Windows; SPSS; Chicago, IL).

294 **RESULTS**

295 *Horizontal FV and PV profile*

296 Table 1 shows the mean mechanical variables from the horizontal FV and PV profile, as well
297 as the 5 and 30-m sprint times, while table 2 shows the lower limb muscle architecture,
298 morphology, and fiber typology values. Univariable analyses indicated that muscle volumes of
299 the GMAX, ADD, RF, VM, VI, sartorius, and iliacus, thickness of GL and GM, and GM
300 pennation angle were all positively associated with hFO ($N \cdot kg^{-1}$; $r = 0.431 - 0.579$; $p < 0.05$;
301 table 3). Muscle volumes of the BFSH, ADD and VM, in addition to BFLH fascicle length,
302 and GM carnosine Z-score were all significantly positively associated with hVO ($m \cdot s^{-1}$; $r =$
303 $0.513 - 0.678$; $p < 0.05$). $hPmax$ ($W \cdot kg^{-1}$) was significantly positively associated with the
304 muscle volumes of BFLH, ADD, RF, VM, VI, TFL, sartorius and iliacus, as well as GM
305 carnosine Z-score and BFLH fascicle length ($r = 0.485 - 0.669$; $p < 0.05$).

306 Figure 2 and table 4 shows the results of the multiple linear regression models demonstrating
307 the combination of muscle characteristics that explained the greatest variation in horizontal FV
308 and PV mechanical variables. Variation in hFO ($N \cdot kg^{-1}$) was best explained by the combination
309 of ADD and VM muscle volume (adjusted $r^2 = 0.432$, $p = 0.007$), while variation in hVO ($m \cdot s^{-1}$)
310 was best explained by the combination of GM carnosine Z-score and BFSH muscle volume
311 (adjusted $r^2 = 0.590$, $p < 0.001$). Variation in $hPmax$ ($W \cdot kg^{-1}$) was best explained by a three-
312 parameter model including the combination of GM carnosine Z-score and ADD and VI muscle
313 volume (adjusted $r^2 = 0.634$, $p = 0.032$). The standardized beta coefficients for each regression
314 model suggested that each muscle characteristic included in each model exerted a similar
315 influence on the given mechanical parameter. Figure 3 shows typical traces of horizontal FV

316 and PV relationships for subjects with similar lower limb muscle volume but divergent in
317 muscle fiber typology (panel A; subject A and B) and for subjects with similar muscle fiber
318 typology but divergent in lower limb muscle volume (panel B; subject C and D).

319 *Vertical FV and PV profile*

320 Table 1 shows the mean mechanical variables from the vertical FV and PV profile, as well as
321 jump height. Univariable analyses indicated that the muscle volume of the ADD, RF, VL, VI
322 and GM thickness were all significantly positively associated with $vF0$ ($r = 0.479 - 0.548$; $p <$
323 0.05 ; table 3). GL pennation angle and GM carnosine Z-score were significantly positively
324 associated with $vV0$ ($r = 0.493 - 0.762$; $p < 0.05$). $vPmax$ was significantly positively associated
325 with the muscle volume of the VL as well as the GM carnosine Z-score ($r = 0.581 - 0.647$; p
326 < 0.01 ; table 3).

327 Figure 2 and table 4 shows the results of the multiple linear regression models demonstrating
328 the combination of muscle characteristics that explained the greatest variation in vertical FV
329 and PV mechanical variables. Variation in $vF0$ was best explained by RF and VL muscle
330 volume ($r^2 = 0.430$; $P = 0.008$), while variation in $vV0$ was best explained by variation in GM
331 carnosine Z-score ($r^2 = 0.580$, $p < 0.001$). Variation in $vPmax$ was most associated with the
332 variation in GM Z-score and VL muscle volume ($r^2 = 0.440$; $P = 0.006$). The standardized beta
333 coefficients for each regression model suggested that each muscle characteristic included in
334 each model exerted a similar influence on the mechanical parameter.

335 **DISCUSSION**

336 As far as the authors' are aware, this is the first study to employ non-invasive techniques to
337 explore the underpinning muscle characteristics of the horizontal and vertical FV and PV
338 relationships during sprinting and jumping. The key findings are: i) a higher GM carnosine Z-
339 score (i.e., greater estimated proportion of type II fibers) was associated with greater $vV0$, $hV0$,

340 vP_{max} and hP_{max} values, and; ii) greater knee extensor muscle volume was associated with a
341 higher $vF0$ and vP_{max} , and ADD and knee extensor volume contributed to the explained
342 variation in $hF0$ and hP_{max} . These findings suggest that muscle fiber typology is a key
343 determinant of vP_{max} and hP_{max} by influencing $V0$, while the volume of specific lower limb
344 muscles are key determinants of P_{max} by influencing $F0$.

345 **Muscle fiber typology**

346 In support of our hypotheses, univariable and multiple linear regression models showed that
347 muscle fiber typology of the GM explained a substantial magnitude of the variation of $V0$ and
348 P_{max} during both sprinting and jumping. There are several lines of evidence that support these
349 findings derived directly from experiments on single muscle fibers and from studies employing
350 multi-joint dynamic exercise. At a single fiber level, Bottinelli et al. (36) found that the
351 maximum shortening velocity (i.e., $V0$) and P_{max} of type II fibers was consistently higher than
352 type I fibers from rat soleus, extensor digitorum longus and plantaris muscles, as well as fibers
353 from the human VL (37). Tihanyi et al. (38) demonstrated that well-trained jump athletes who
354 possessed more than 50% type II fibers in the VL were able to generate a higher velocity, and
355 more power, during knee extension exercise compared to athletes who possessed less than 50%
356 type II fibers. Furthermore, there were significant correlations between the percentage of type
357 II fibers and power, as well as velocity, at the four highest loads. In the present study, muscle
358 fiber typology did not contribute to the multiple linear regression models explaining the
359 variation in $vF0$ and $hF0$ values. This finding is also supported by single fiber studies that
360 indicate $F0$ is not consistently different between fiber types (39, 40). Based on previous
361 research (15), and the findings from the present study, it is reasonable to suggest that possessing
362 a higher proportion of type II fibers would be beneficial for sprints of longer duration. This
363 hypothesis could be supported by the relationship between muscle fiber typology and the
364 mechanical variables underpinning sprint performance (i.e., hP_{max} and $hV0$), given that these

365 variables are strongly associated with sprints of longer duration (i.e., mean 100-m speed and
366 4-s sprinting distance), whereas *hFO* is not (41, 42). During the latter stages of a sprint when
367 maximal velocity is being approached, the short ground contact time and resultant contraction
368 time does not allow for maximal muscle force to be reached (43), and the rate of force
369 development is more important. During this stage of sprinting, possessing a higher estimated
370 proportion of type II fibers would promote the ability to continue to produce force at high
371 velocities and achieve a greater *hVO*. Akin to single muscle fiber experiments, both type IIa
372 and IIx fibers can produce more force at higher shortening velocities than type I fibers (37, 39),
373 which may underpin the association found in the present study between muscle fiber typology
374 and *hVO*. It should be noted that our estimation of muscle fiber typology in the GM, likely
375 reflects the typology of other prominent lower limb muscles. There appears to be an across-
376 muscle phenotype, whereby individuals who express a high proportion of a given fiber type
377 proportion in one muscle also express a comparably high proportion of the same fibre type in
378 other muscles (44). Nonetheless, the measurement of muscle fiber typology in other lower limb
379 muscles may have added value in the present study. Our findings demonstrate a clear advantage
380 for athletes competing in explosive sports who possess fast muscle fiber typology.

381 **Muscle volume**

382 Given that muscle volume is a well-recognised determinant of its force generating capacity
383 (20), it was not surprising that we observed a number of lower limb muscles displaying a
384 positive association with both *hFO* and *vFO*. In further support of our hypotheses, the multiple
385 linear regression models revealed that the volume of the ADD and knee extensor muscles were
386 key determinants of *FO* during both sprinting and jumping, thus influencing *vPmax* and *hPmax*.
387 While few studies have associated lower limb muscle volumes with mechanical variables from
388 the horizontal FV and PV profiles directly, our findings agree with cross-sectional studies that
389 have reported most hip and knee-crossing muscles to be significantly larger in sprinters

390 compared to recreationally active individuals (11) and endurance runners (12). In particular,
391 sprinters possess significantly larger vastus medialis (30%) and adductor magnus, longus and
392 brevis (22 – 26%) muscles than non-sprinters when normalised to height and mass. More recent
393 work (18) reported that hip extensor muscles were substantially larger (+32%) in elite (10.10
394 \pm 0.07 s 100 m sprinters) compared to sub-elite sprinters (10.80 \pm 0.30 s). Interestingly, this
395 study (18) reported that GMAX alone explained 34-44% of the variation in season best 100 m
396 sprint performance. In agreement with this study and our hypothesis, we found that GMAX
397 volume was significantly associated with *hFO*, but it did not contribute to the multivariable
398 regression model, whereby ADD and VM volume explained the most variation in *hFO*. In
399 support, Sugisaki et al. (25) reported that variation in 30-m sprint running time was best
400 explained by the anatomical CSA of the ADD. Given that we found the ADD to be a significant
401 determinant of *hFO*, it is probable that the ADD are important muscles for sprint acceleration.
402 This importance may arise from the contribution of the ADD to hip extension torque during
403 the late-swing to early-contact phase of sprint acceleration (25). Adductor magnus acts as a hip
404 extensor through the entire hip joint range of motion, while the adductor brevis and longus also
405 act as hip extensors when the hip is flexed more than 25° and 50°, respectively (25, 45).
406 Furthermore, the high degrees of hip flexion experienced during acceleration may increase the
407 mechanical effectiveness of adductor magnus and reduce the effectiveness of GMAX via
408 alterations to moment arms (45). In addition to the ADD, the volume of the VM contributed to
409 the regression model explaining variation in *hFO*. Previous research has reported that maximal
410 isokinetic knee extensor torque is negatively correlated with 15 m sprint time (46), whereby
411 knee extensor torque is thought to contribute to the swing and stance phases during sprinting
412 (26). These findings, along with those of the present study, highlight the important role of the
413 knee extensors during the acceleration phase of sprinting. We found that the volume of the
414 BFSH significantly contributed to the regression model explaining the variation in *hVO* in

415 sprinting. Previous research (47) has shown that a greater amount of horizontal force (averaged
416 over an entire sprint acceleration) was found in subjects who had greater BF activation just
417 before ground contact and superior eccentric hamstring torque. These findings show the
418 important role that the BF has during sprint running. Future work should seek to determine
419 whether interventions targeted at promoting hypertrophy in the muscles associated with the
420 mechanical parameters underpinning the horizontal FV and PV profiles leads to an
421 improvement in sprint acceleration. Lastly, in agreement with our hypotheses, we found that
422 the volume of plantar flexor muscles were not associated with variation in the mechanical
423 parameters of the FV and PV profiles.

424 **Muscle architecture**

425 In the present study, muscle architecture only explained a small amount of variation in the
426 maximal mechanical parameters of the horizontal or vertical FV or PV profiles. Specifically,
427 univariable analyses revealed that BFLH fascicle length was associated with a greater hVO and
428 $hPmax$, while the thickness of the GL and GM were associated with hFO (GM and GL) and
429 vFO (GM). These findings only partly agreed with our hypotheses, as we surmised that the
430 fascicle length of all lower limb muscles that we measured would be associated with hVO and
431 $hPmax$. Theoretically, muscles with longer fascicles, and presumably more sarcomeres in
432 series, exhibit higher shortening velocities (when completely unloaded) and greater
433 contractility than muscles with shorter fascicles (20). Consequently, longer fascicles within the
434 BFLH may improve the rate at which the forward swinging lower limb is decelerated during
435 the late swing phase of sprinting, which may contribute to greater velocities via increasing
436 stride frequency. Greater rates of BFLH shortening may also contribute to an enhanced hip
437 extensor moment during sprinting and jumping. While these hypotheses require further
438 investigation, it is important to consider that fascicle lengths of the VL, GM and GL were not
439 associated with the mechanical variables of the vertical or horizontal FV and PV profile in the

440 current study. Recent work (21) reported that GM muscle fascicle length accounted for almost
441 half of the difference in $V0$ between young and old men derived from the plantarflexion torque-
442 velocity relationship. However, in the current study, FV and PV profiles were determined
443 during the multi-joint, dynamic movements of sprinting and jumping, compared to the torque-
444 velocity relationships derived from single joint movements of the ankle dorsiflexors.
445 Interestingly, studies from the same research group (10, 14) reported longer GM, GL and VL
446 muscle fascicles in male sprinters (10) compared to distance runners and non-athletes, and in
447 fast (10.0 – 10.9 s 100-m sprinters) compared to slow sprinters (11.0 – 11.7 s) (14).
448 Furthermore, pennation angle ($r = 0.34$ to 0.46 , $p < 0.05$) and muscle fascicle length ($r = -0.40$
449 to -0.54 , $p < 0.05$) were associated with personal best 100-m times (14). These findings would
450 suggest that these muscle architectural characteristics may underpin the mechanical variables
451 from the horizontal FV and PV profile given their relationship to sprint performance (41, 42).
452 Despite this premise, we had a smaller sample size compared to these studies (10, 14), other
453 studies did not employ measures of actual performance or mechanical variables (10) and it may
454 not be appropriate to compare elite 100 m sprinters (10, 14) with sub-elite rugby league
455 athletes. Interestingly, we observed that greater thickness but not volume of the GM and GL
456 muscles was associated with $hF0$. While this observation may be difficult to reconcile, it is
457 consistent with previous work. For example, Abe et al. (10) and Kumagai et al. (14) both
458 reported that sprint trained athletes had thicker GL muscles than sedentary controls. However,
459 Handsfield et al. (11) found no significant difference in GL (7%) or GM (4%) muscle volumes
460 (normalised to body size) when comparing sprinters to non-sprinters. These data suggest the
461 possibility that the muscle bellies of these muscles may be relatively short despite still having
462 a large physiological cross-sectional area, but this notion requires further investigation. One
463 previous study (22) has shown that quadriceps thickness and VL pennation angle explained
464 ~62% of the variation in $vF0$ estimated from loaded and unloaded countermovement jumps.

465 Fiber pennation increases a muscle's physiological cross-sectional area (via increasing the
466 number of sarcomeres in parallel), which is proportional to its force generating capacity (23).
467 As such, a greater pennation angle is likely to be associated with a greater volume of muscle.
468 While we did not observe any association between VL pennation angle or thickness and vFO
469 which disagreed with our hypotheses, we did find that VL volume (along with RF) contributed
470 to the regression model explaining ~43% of the variation in vFO . Differences in the type of
471 jump that was employed (squat or countermovement jump), or the way in which muscle
472 architecture was quantified may have contributed to the lack of association that we found with
473 the architecture of the VL in the present study compared to that of Morales-Artacho et al. (22).
474 The latter study measured muscle thickness at the middle and proximal regions of the VM, VL,
475 RF and VI to provide a measure of mean quadriceps muscle thickness and pennation angle of
476 the VL was taken as the average value from 3 sites (e.g. at 20, 50 and 60% of thigh length),
477 while we relied on a single measurement site of the VL. Given that muscle thickness and
478 pennation angle measurements vary along the length of the muscle, muscle architecture
479 measurements at multiple sites within a muscle may be necessary to reduce some of the within-
480 muscle variability. Nonetheless, given that the overall volume of a muscle is directly related to
481 its force generating capacity (20), our hypothesis was confirmed whereby the volume of the
482 knee extensor muscles to explain a substantial amount of the variability in vFO and $vPmax$.

483 **Limitations**

484 There are some limitations of this study that should be acknowledged. First, the ultrasound
485 field of view could not capture the entire length of fascicles, and as a consequence, fascicle
486 length was estimated using extrapolation methods (34). While this estimation technique has
487 been validated against cadaveric measurements (48), it was recently shown that this approach
488 overestimated BFLH fascicle length when compared with extended field of view scans (49).
489 At present, extended field of view imaging has not been validated against cadaveric data, so

490 the current methodology should not be considered inferior. The extrapolation methods
491 employed in the present study have high levels of inter-day reliability in our lab (ICC >0.95
492 and CV <6%) for muscle fascicle length measurements of the GM, GL, VL and BFLH.
493 Nonetheless, muscle architecture measures were only performed at a single location in four
494 lower limb muscles, which may have limited the strength of the associations with horizontal
495 and vertical FV and PV mechanical parameters compared to a previous study (22). Our
496 estimation of muscle fiber typology is based on the ¹H-MRS measurement of muscle carnosine
497 which is a stable dipeptide that is present in two-fold higher concentrations in type II fibers and
498 is positively correlated (P = 0.009 and r = 0.714) with the muscle biopsy determined proportion
499 of type II fibers (27). When this association is translated to explained variance (i.e., r²), ~50%
500 of the variability in muscle fiber typology (i.e., myosin heavy chain composition) is not
501 explained by variation in muscle carnosine content. It should be noted that a large portion of
502 this unexplained variation may be due to the lower levels of reliability of the methods used to
503 determine myosin heavy chain composition given that we showed extremely high levels of
504 reliability between inter-day ¹H-MRS measurements of muscle carnosine (CV = 4.3%). Indeed,
505 a recent study (50) demonstrated that the inter-biopsy variation (CV) in MHC type I, IIa and
506 IIx fibers was 21.5%, 15.4% and 42.0%, respectively. In addition, ¹H-MRS samples both
507 superficial and deep parts of the muscle as well as a substantially larger volume of muscle
508 compared to a muscle biopsy which may also contribute to the unexplained variation between
509 measurements. Lastly, we report a large number of correlation analyses, some of which fall
510 outside of the scope of our hypotheses which may result in a type I error inflation, and so their
511 interpretation should be done with caution.

512 **Conclusions**

513 This study demonstrates that lower limb muscle characteristics are associated with the
514 mechanical parameters of the FV and PV profiles in sub elite rugby league players. Muscle

515 fiber typology and specific lower limb muscle volumes are major determinants of vP_{max} and
516 hP_{max} , by influencing V_0 and F_0 , respectively. While muscle architectural characteristics did
517 not seem to be as deterministic as other muscle characteristics, BFLH fascicle length was
518 associated with a greater hV_0 and hP_{max} and the thickness of the GL and GM were associated
519 with hF_0 and vF_0 . These findings may inform the design of targeted training programs to
520 maximise sprint and jump performance in athletes.

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FIGURES:

Figure 1 - Participants underwent magnetic resonance (MR) imaging of their entire lower limb to determine muscle volumes of the major hip, knee and ankle-spanning muscles. Muscles were segmented in axial MR images from the hip (panel A and B), the thigh (panel C) and the shank (panel D). Muscle volume was calculated by multiplying the inter-slice distance by the sum of the cross-sectional area of the total number of traced slices (panel E; semitendinosus). Muscle thickness, fascicle pennation angle and fascicle length were measured by B-mode ultrasonography of the vastus lateralis, biceps femoris long head and gastrocnemius lateralis and medialis (panel F). We also used proton MR spectroscopy ($^1\text{H-MRS}$) to quantify the carnosine content in the gastrocnemius medialis in order to estimate muscle fiber typology. We also used proton MR spectroscopy ($^1\text{H-MRS}$) to quantify the carnosine content in the gastrocnemius medialis in order to estimate muscle fiber typology. Panel G and H show a coronal and transverse MR image to demonstrate the localization of the voxel, while panel I shows a detailed spectra of the downfield carnosine region.

Figure 2 - Determinants of the mechanical variables derived from the horizontal (panel A) and vertical force-velocity and power-velocity profiles (panel B). Bars indicate the magnitude of explained variance ($\% r^2$) obtained from multivariable linear regression analyses with the combination of predictors presented at the top of each bar.

Figure 3 - Typical traces of linear force–velocity and 2nd degree polynomial power–velocity relationships obtained from overground sprinting for subjects with similar lower limb muscle volume but divergent in muscle fiber typology (panel A; subject A and B) and for subjects with similar muscle fiber typology but divergent in lower limb muscle volume (panel B; subject C and D). Typically, subjects with a higher estimated proportion of type II fibers (i.e., higher carnosine Z-score) possessed a greater horizontal $V0$ and $Pmax$ (i.e., subject A) compared to those with a lower estimated proportion of type II fibers. Subjects with greater lower limb muscle volume possessed a greater horizontal $F0$ and $Pmax$ compared to those with a smaller lower limb muscle volume. In particular, the volume of the adductors and vastus intermedius ($Pmax$) and vastus medialis ($F0$) seemed to be most influential on the maximal mechanical parameters.

TABLES:

Table 1 - Mechanical variables derived from the vertical (i.e., v) and horizontal (i.e., h) force-velocity and power-velocity relationship as well as 5 m and 30 m sprint times and jump height.

Table 2 – Lower limb muscle architecture, morphology, and fiber typology values.

Table 3 – Pearson correlation values between the lower limb muscle characteristics and the mechanical variables derived from the horizontal and vertical force-velocity and power-velocity relationships.

^aIndicates $P < 0.05$, ^bIndicates $P < 0.01$, ^cIndicates $P < 0.001$

Table 4 - Stepwise linear regression model parameter estimates for the relationship between the vertical and horizontal FV and PV mechanical variables (dependent variables) and muscle architecture (i.e., fascicle length, pennation angle and thickness), morphology (i.e., muscle volume) and fiber typology (gastrocnemius carnosine Z-score).