



## LJMU Research Online

**Brennan, SF, Cresswell, AG, Farris, DJ and Lichtwark, GA**

### **The Effect of Cadence on the Mechanics and Energetics of Constant Power Cycling**

<http://researchonline.ljmu.ac.uk/id/eprint/10294/>

#### **Article**

**Citation** (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

**Brennan, SF, Cresswell, AG, Farris, DJ and Lichtwark, GA (2018) The Effect of Cadence on the Mechanics and Energetics of Constant Power Cycling. Medicine & Science in Sports & Exercise. ISSN 0195-9131**

LJMU has developed **LJMU Research Online** for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact [researchonline@ljmu.ac.uk](mailto:researchonline@ljmu.ac.uk)

<http://researchonline.ljmu.ac.uk/>

1 **The Effect of Cadence on the Mechanics and Energetics of Constant Power Cycling**

2

3 **Running title:** Effect of cadence on mechanics and energetics

4

5 Scott F. Brennan<sup>1,2</sup>, Andrew G. Cresswell<sup>1</sup>, Dominic J. Farris<sup>1,3</sup>, and Glen A. Lichtwark<sup>1</sup>

6

7 <sup>1</sup>The University of Queensland, School of Human Movement & Nutrition Sciences, Centre for

8 Sensorimotor Performance, Brisbane, Australia; <sup>2</sup>Liverpool John Moores University, Sport and

9 Exercise Sciences, Liverpool, United Kingdom; <sup>3</sup>University of Exeter, Sport and Health Sciences,

10 Exeter, United Kingdom

11

12 **Corresponding author:**

13 Scott F. Brennan

14 Liverpool John Moores University

15 Sport and Exercise Sciences

16 Tom Reilly Building, Byrom Street, Liverpool, L3 3AF

17 United Kingdom

18 email: S.Brennan@ljmu.ac.uk

19 phone: (+44) 151 904 8094

20

21

22 SF Brennan was supported by an Australian Postgraduate Award scholarship during the completion of this project.

23 This project did not receive any external funding but did receive internal funding for the purchase of equipment.

24 **Conflict of Interest:** The authors have no conflicts of interest to declare with professionals, companies or

25 manufacturers who may benefit from the results of the present study. The results of the present study do not constitute

26 endorsement by ACSM. The results of the study are presented clearly, honestly, and without inappropriate data

27 manipulation.

28 **Abstract**

29 At a constant power output, cyclists prefer to use a higher cadence than those that minimise  
30 metabolic cost. The neuromuscular mechanism underpinning the preferred higher cadence remains  
31 unclear. **Purpose.** The aim of this study was to investigate the effect of cadence on joint level work  
32 and vastus lateralis (VL) fascicle mechanics while cycling at a constant, submaximal, power  
33 output. We hypothesised that preferred cycling cadence would enhance the power capacity of the  
34 VL muscle when compared to a more economical cadence. Furthermore, we predicted that the  
35 most economical cadence would coincide with minimal total electromyographic activity from the  
36 leg muscles. **Methods.** Metabolic cost, lower limb kinematics, joint level work, VL fascicle  
37 mechanics, and muscle activation of the VL, rectus femoris, biceps femoris, gastrocnemius  
38 medialis and soleus muscles were measured during cycling at a constant power output of 2.5 W/kg  
39 and cadences of 40, 60, 80 and 100 revolutions per minute (RPM). A preferred condition was also  
40 performed where cadence feedback was hidden from the participant. **Results.** Metabolic cost was  
41 lowest at 60 RPM, but the mean preferred cadence was 81 RPM. The distribution of joint work  
42 remained constant across cadences, with the majority of positive work being performed at the knee.  
43 The preferred cadence coincided with the highest VL power capacity, without a significant penalty  
44 to efficiency, based on fascicle shortening velocity. **Conclusions.** Cycling at a higher cadence is  
45 preferred to ensure that the muscle's ability to produce positive power remains high. Further  
46 investigations are required to examine what feedback mechanism could be responsible for the  
47 optimisation of this motor pattern.

48

49 **Keywords:** vastus lateralis, work, power, efficiency, ultrasound, electromyography

50

51 **Introduction**

52 Humans are generally good at reducing metabolic cost for rhythmic movements, such as walking  
53 and running, by selecting a movement pattern that minimises energy expenditure at the required  
54 speed (1). However, both trained and untrained cyclists prefer to use cadences higher than those  
55 that minimise energy expenditure (2), suggesting that other factors influence the selection of the  
56 preferred cycling cadence.

57

58 Cycling provides a convenient movement pattern to examine the relationship between preferred  
59 movement, metabolic cost and muscle-tendon mechanics. The body's centre of mass moves very  
60 little relative to the bicycle in seated cycling, while the lower limb muscles perform work to  
61 overcome rolling and air resistance. In contrast to walking or running on a level surface, which  
62 requires negligible net work per cycle, cycling at a constant power output requires net positive  
63 work to be performed against the resistance provided at the cranks; the majority of which is  
64 performed by the knee and hip extensors (3,4). It is also possible to manipulate both resistance and  
65 cadence to maintain the same overall power output. For example, cycling with a low cadence and  
66 high pedal forces may produce the same power output as cycling with high cadence and low pedal  
67 forces. In both conditions, the joint ranges of motion remain relatively similar and only the velocity  
68 of movement varies. What is unclear is how the force and velocity requirements of the hip, knee  
69 and ankle muscles change with factors such as cadence, and how this might influence the preferred  
70 and/or most economical movement pattern.

71

72 Generally, the central nervous system is able to achieve the same overall mechanical output using  
73 many different motor strategies. Different strategies during cycling could change the distribution

74 of power between joints, which would likely impact the metabolic cost of performing the  
75 movement because it relates to lower limb muscle performance (5). The sum of the lower limb  
76 average joint moments has been shown to decrease at higher cadences (6), indicating a reduced  
77 workload for the associated muscles. Forward dynamics simulations of cycling have shown an  
78 optimal cadence of 90 RPM at a relatively high power output (~3.5 W/kg). At this optimal cadence,  
79 which is similar to the preferred cadence for the power output assessed, neuromuscular parameters  
80 (e.g. muscle force, activation, stress) were minimised compared to lower or higher cadences (7).  
81 Combined with a close association between the most economical cadence and total average muscle  
82 activation (8), these results would suggest that the preference for cadences above the most  
83 economical may be related to muscle mechanical requirements and their activation conditions,  
84 rather than energetic cost.

85

86 Skeletal muscle has a limited capacity for force production that depends on the length and  
87 shortening velocities of the fibres. The fibres of each muscle have an optimum length for force  
88 production and will experience a hyperbolic decrease in force capacity as shortening velocity  
89 increases (9,10). The amplitude and velocity of muscle fibre shortening are therefore critical to a  
90 muscle's capacity to produce force and power during movements like cycling (11). These factors  
91 are also critical for determining the power output and efficiency of a muscle (12,13). Depending  
92 on the activation conditions, peak muscle power may be observed at faster shortening velocities  
93 than peak efficiency (12,13). As such, it may not be possible to maximise power and efficiency at  
94 the same cadence, which may impact on a cyclist's preferred cadence during cycling.

95

96 There were two main aims of this study: (1) to determine the effects of cadence on metabolic cost,  
97 joint level mechanical work, and cumulative muscle activation while cycling at a constant  
98 submaximal power output; (2) to determine the effect of cadence on vastus lateralis (VL) muscle  
99 fascicle mechanics and assess the implications for muscle power and efficiency. The fascicle  
100 mechanics of VL would be used as a representative muscle for the contractile mechanics of the  
101 quadriceps muscles. We hypothesised that the preferred cadence would be higher than the cadence  
102 that minimises metabolic cost and overall muscle activation, as has been reported previously (2),  
103 but that there would be no significant change in the distribution of joint work between the hip,  
104 knee and ankle with changes in cadence, because of the constraints of the pedal trajectory. On the  
105 basis that favourable muscle contractile dynamics is linked to overall metabolic economy, we  
106 hypothesised that the most economical cadence would coincide with VL shortening velocities that  
107 are most favourable for efficiency, which would minimise cumulative muscle activation of the VL.  
108 Since higher cadences should require higher muscle shortening velocities, we also hypothesised  
109 that the preferred cadence would require VL shortening velocities that are more favourable for VL  
110 power production.

111

## 112 **Methods**

113 Participants for this study were recruited from the staff and students of The University of  
114 Queensland. Ethical approval was granted from the institutional ethics committee. Written  
115 informed consent was obtained from the participants before commencing the experiment.  
116 Participants included 14 healthy adults (11 male, 3 female) that were capable but not competitive  
117 cyclists. The mean ( $\pm$  SD) age, height, and mass of all participants was  $28 \pm 5$  years,  $178 \pm 6$  cm,  
118 and  $76 \pm 9$  kg, respectively.

119

120 This study utilised some muscle level data previously presented in Brennan et al. (2018), however  
121 additional data was also collected and analysed to achieve the unique aims of the current study  
122 (11).

123

#### 124 Muscle force-length-velocity relationship

125 The method for determining the relationship between quadriceps force and VL fascicle length  
126 (isometric contractions) and velocity (isokinetic contractions) has been outlined in detail in  
127 Brennan et al. (2018); it is briefly detailed below (11).

128

129 After a familiarisation session (1-2 days prior to the experimental data collection) participants were  
130 seated in a dynamometer (HUMAC NORM, CSMi Inc., Stoughton, MA, USA) with a trunk angle  
131 of  $80^{\circ}$  ( $10^{\circ}$  from upright) and adjusted to align the axle of the motor with the rotation axis of the  
132 left knee. After a standardised warm-up, participants performed three maximal effort, isometric  
133 contractions from  $50^{\circ}$  to  $100^{\circ}$  of knee flexion in  $10^{\circ}$  increments, in a randomised order ( $0^{\circ}$  = full  
134 knee extension). A 120 s period of rest was given between trials to avoid potential fatigue effects.  
135 Participants then performed three, maximal effort, isokinetic knee extensions from  $100^{\circ}$  flexion to  
136 full extension at angular velocities of  $50^{\circ}/s$ ,  $100^{\circ}/s$ ,  $200^{\circ}/s$ ,  $300^{\circ}/s$ , and  $400^{\circ}/s$ , in a randomised  
137 order. A movement initiation threshold was set at 90% of the maximum isometric torque recorded  
138 at the  $100^{\circ}$  knee angle.

139

140 Knee extensor torque and joint angle were recorded at 2 kHz during each contraction (CED Micro  
141 1401 A/D converter and Spike 2 software, Cambridge Electronic Design Ltd., Cambridge,

142 England). The measured torque was corrected to account for the effect of gravity at different joint  
143 angles. To remove any inertial effects on the measured torque during acceleration of the  
144 dynamometer attachment, the mean torque and fascicle shortening velocity were measured during  
145 only the true isokinetic (constant angular velocity) portion of the movement.

146

147 Ultrasound images of VL muscle fascicles as well as its deep and superficial aponeuroses were  
148 simultaneously recorded with B-mode ultrasound using two flat ultrasound transducers  
149 (LogicScan 128, LV7.5/60/96Z transducers, 5 MHz central frequency, image depth of 50 mm and  
150 sample rate of 80 Hz, TELEMED, Vilnius, Lithuania) that were held end-to-end in a custom frame  
151 and secured to the lateral thigh (14). Markings were made on the skin with a semi-permanent  
152 marker so the position of the transducers could be replicated for the cycling protocol. Fascicle  
153 length changes during contractions were measured offline using a custom Matlab script  
154 (MathWorks Inc., Natick, USA) that used a semi-automatic tracking algorithm (15,16). Manual  
155 corrections of the fascicle end points were made if the tracking algorithm could not adequately  
156 detect fascicle length change from one frame to the next (assessed by the operator).

157

158 Quadriceps force was calculated as knee extensor joint torque divided by the angle specific  
159 moment arm, which was measured from a scaled musculoskeletal model created for each  
160 participant from the cycling data collection (17). Subject-specific force-length and force-velocity  
161 curves were produced using physiologically appropriate models as described thoroughly in  
162 Brennan et al. (2018) (11). Briefly, at each joint angle the maximum quadriceps force and  
163 corresponding fascicle length during isometric contraction was determined, based on two trials,  
164 and the relationship between force and fascicle length was fit (least square) with a parabolic



165 function (18) for each participant. During the isokinetic contractions, the mean quadriceps force  
166 and corresponding fascicle shortening velocity was determined during the true isokinetic portion  
167 of the trial, to avoid any inertial effects. The maximum mean force produced from two trials at  
168 each velocity was used in a least square fit of a force-velocity relationship (19) for each participant.  
169 The goodness of fit was calculated separately for each participant.

170

### 171 Muscle power-efficiency relationship

172 Fascicle power-velocity and efficiency-velocity curves were generated for each individual. The  
173 power curve was generated as the product of force and velocity, based on the curve fit to the  
174 experimental data. The relationship between shortening velocity and muscle efficiency was  
175 generated using a model described by Lichtwark & Wilson (20). In this model, efficiency was  
176 defined as the muscle work produced divided by the energetic cost of performing that work  
177 (Efficiency = Work / [Heat + Work]). Work was defined as the time integral of the force multiplied  
178 by the velocity. Heat is the combination of heat generated to maintain an isometric force plus the  
179 heat of shortening. The rate of heat production was estimated from  $V_{max}$  and curvature of the force-  
180 velocity relationship ( $G$ ) taken from the individual force-length and force-velocity curves.  
181 Assuming a maximum crossbridge activation rate, the maintenance heat rate was calculated as 8  
182 ( $V_{max}/G^2$ ) and shortening heat as  $V_{CE}/G$  (where  $V_{CE}$  is the instantaneous velocity of the contractile  
183 element). The efficiency was therefore equal to work divided by the sum of the maintenance heat,  
184 shortening heat, and work at each point on the velocity curve.

185

186

187 Cycling joint and muscle function

188 *Protocol*

189 The cycling protocol consisted of two sessions. In the first session, steady state oxygen  
190 consumption was measured (see *Metabolic Cost* below) during seated cycling on an ergometer  
191 (Lode Excaliber Sport, Lode B.V., Groningen, Netherlands) at a constant power output of 2.5  
192 W/kg body mass, at predetermined cadences of 40 revolutions per minute (RPM), 60 RPM, 80  
193 RPM and 100 RPM. A preferred condition was also completed, where cadence feedback was  
194 hidden and participants were instructed to cycle at the cadence that felt the “most comfortable”.  
195 The order of conditions was randomised. Shimano SPD-SL pedals and R078 cycling shoes were  
196 used for all conditions (Shimano Inc., Osaka, Japan). Seat height was normalised to 100%  
197 trochanter length (21), measured as the vertical distance from the greater trochanter to the base of  
198 the foot when standing. In the second session, surface electromyography (EMG) of leg muscles  
199 [VL, rectus femoris (RF), biceps femoris (BF), medial gastrocnemius (MG), and soleus (SOL)],  
200 three-dimensional (3D) kinematics of the lower limb, pedal force measurement using instrumented  
201 cranks (Swift Performance, Brisbane, Australia), and VL muscle fascicle length changes using B-  
202 mode ultrasonography were recorded while completing the same protocol and order of conditions.  
203 Data capture was synchronised using a logic pulse generated by the ultrasound to trigger data  
204 collection of the motion capture and EMG systems. Participants cycled at the target cadence for a  
205 minimum of 120 s and they could maintain a constant cadence ( $\pm 5$  RPM). Data were recorded for  
206 a minimum of five pedal revolutions. The absolute time of the five revolutions varied across  
207 cadence conditions. Between conditions, participants cycled at 50 W at a self-selected cadence for  
208 120 s of active rest.

209

210 *Metabolic cost*

211 Metabolic data was collected using open circuit spirometry (Vacumed Vista-MX2, Vacumetrics  
212 Inc., Ventura, California, USA).  $\dot{V}O_2$  and  $\dot{V}CO_2$  were measured continuously during exercise. The  
213 gas analysers were calibrated immediately prior to testing and validated between each condition  
214 using certified calibration gases to remove drift. The turbine calibration was checked prior to  
215 testing using a 3 L syringe. Resting  $\dot{V}O_2$  was measured while seated on the bike for 3 to 5 minutes  
216 prior to the cycling protocol. Participants performed a brief warm up for 3 minutes at 100 W at a  
217 self-selected cadence while the experimental protocol was explained to them in detail. Participants  
218 cycled at the prescribed cadence for a minimum of 5 minutes to achieve steady state, with an  
219 equivalent rest period between conditions. Steady state was determined by a < 10% difference in  
220  $\dot{V}O_2$  over the final minute. Submaximal oxygen uptake was calculated from the mean  $\dot{V}O_2$  of the  
221 final minute of data when steady state was achieved. Net metabolic power was calculated from  
222 equations based on O<sub>2</sub> consumption and CO<sub>2</sub> production (22).

223

224 *Joint kinematics and kinetics*

225 A six-camera optoelectronic motion analysis system (Qualisys, Gothenburg, Sweden) was used to  
226 capture the locations of 23 passive, reflective markers positioned on anatomical landmarks on the  
227 pelvis, left thigh, left shank and left foot at a sample rate of 200 Hz. Scaling markers were placed  
228 on the anterior and posterior iliac spines, greater trochanter, medial and lateral epicondyles, medial  
229 and lateral malleoli, calcaneus, 1<sup>st</sup> and 5<sup>th</sup> metatarsal heads. A static calibration capture was  
230 collected while standing upright with arms crossed to opposite shoulder. A custom Matlab script  
231 was used to scale the model size and segmental inertial parameters in OpenSim software v3.3 on  
232 a modified version of the OpenSim *gait 2392* model (23). Additional clusters of dynamic tracking

233 markers mounted on semi-rigid plates were placed on the lateral mid-thigh, and mid-shank for  
234 movement trials. Kinematic data was exported for analysis using Matlab and OpenSim. Radial and  
235 tangential crank forces as well as crank position were measured from the instrumented cranks  
236 (Swift Performance, Brisbane, Australia). The forces were transformed from the crank frame of  
237 reference to the global coordinate system using standard rotation matrices and the crank angle. The  
238 resultant pedal reaction force was applied to the foot segment of the rigid body model, using an  
239 inverse dynamics approach to calculate joint moments. Joint mechanical power was calculated as  
240 the product of the calculated joint moment and angular velocity. Joint mechanical work per  
241 revolution was calculated as the time integral of mechanical power per cycle.

242

#### 243 *Fascicle length*

244 Ultrasound images were simultaneously recorded from the VL muscle using the same method as  
245 described earlier. The same two ultrasound transducers were secured to the lateral thigh in the  
246 same location as the dynamometer protocol and the same method for tracking was used. The same  
247 cycles that were analysed for the kinematics/kinetics were analysed to determine change in fascicle  
248 length as a function of crank angle. If a cycle could not be tracked, the next consecutive cycle was  
249 used.

250

#### 251 *Muscle activation*

252 Surface EMG was collected from the VL, RF, BF, MG, and SOL muscles using a wireless EMG  
253 system (Myon 320 system, Myon AG. Baar, Switzerland). Placement of the electrodes was based  
254 on SENIAM guidelines with an inter-electrode distance of 2 cm (24). Electrode sites were shaved,  
255 and cleaned using an abrasive gel (Nuprep Skin Prep Gel, Weaver and Company, Aurora,

256 Colorado, USA) and rubbing alcohol. EMG signals were recorded at 2 kHz. All EMG signals were  
257 digitally band-pass filtered between 15-500 Hz to remove non-physiological signals and offset  
258 removed by subtracting the median activation from the signal for each muscle. The filtered signals  
259 were then processed by calculating the root mean square (RMS) over a moving window width of  
260 50 ms. EMG signals for each muscle were normalized to the mean of the maximal activation per  
261 cycle during the preferred cadence condition. To quantify the amount of muscle activation per  
262 cycle, the EMG signal for each muscle was integrated with respect to time. Cumulative muscle  
263 activation was calculated by multiplying the integrated muscle activation per cycle by the cadence  
264 (RPM) to calculate the cumulative activation per minute. To scale the activation of each muscle to  
265 a physiologically appropriate value before summing to attain total muscle activation, each  
266 muscle's cumulative activation was multiplied by its relative mass (25).

267

#### 268 Analysis

269 VL fascicle lengths and velocities recorded during the cycling task were normalised to optimal  
270 length (from the individual force-length curve) and maximal shortening velocity (from the  
271 individual force-velocity curve), respectively. To determine the effect of cadence on the power  
272 and efficiency of VL, average power and efficiency was calculated from the individual power and  
273 efficiency curves for each cadence. For each cadence condition and each individual participant,  
274 the average power and efficiency during the concentric action of VL were calculated based on the  
275 average normalised velocity during the period when there was a positive knee extension moment  
276 and concomitant fascicle shortening. From here on, power or efficiency capacity refers to the  
277 average value calculated for each condition.

278

279 Statistical comparisons were performed using Graphpad Prism 7 (GraphPad Software Inc., La  
280 Jolla, CA, USA). A repeated measures ANOVA was performed across cadence conditions and  
281 Holm-Sidak multiple comparisons tests were used to compare each of the fixed cadences with the  
282 preferred cadence condition. Alpha was set at 0.05 for all tests. All waveform data is presented as  
283 an average of the crank revolution (top-dead-centre = 0°).

284

## 285 **Results**

286 Of the 14 participants to complete all of the testing sessions, some data had to be removed due to  
287 technical issues, or insufficient ultrasound images to reliably track VL fascicles in all conditions.

288 As a result, 12 data sets were analysed for the metabolic data, 11 for the kinematics and kinetics,

289 10 for muscle fascicle tracking, and 11 for the muscle activation data. In relation to the above, the

290 metabolic energy data (and consequently all cycling data) was excluded if the participant did not

291 reach steady state for all conditions, the kinematic and kinetic data was excluded if the

292 instrumented cranks did not transmit crank force data for all conditions, muscle fascicle data was

293 excluded if it could not be reliably tracked for both the dynamometer and cycling data, and muscle

294 activation data was excluded due to movement artefact or transmitter issues. The mean  $\pm$  SD for

295 age, height and mass of the participants that determined the final results were  $28 \pm 5$  years,  $177 \pm$

296  $6$  cm, and  $73 \pm 7$  kg, respectively.

297

### 298 *Metabolic cost*

299 The mass-relative power output of the protocol required an average power output of  $183 \pm 17$  W.

300 There was a significant main effect of cadence on net metabolic power ( $p < 0.01$ ,  $n = 12$ ) with the

301 minimal metabolic costs occurring at 60 RPM (Figure 1). The preferred cadence was  $81 \pm 12$  RPM.

302 The post-hoc analysis showed significantly lower metabolic cost at 60 RPM and significantly  
303 greater metabolic cost at 100 RPM compared to the preferred cadence.

304

### 305 *Kinematics & Kinetics*

306 The inverse dynamics analysis (n = 11) showed that the knee extensors produced a large joint  
307 moment during the first half (down-stroke) of the pedal revolution (Figure 2a). There was a  
308 systematic decrease in peak hip extension, knee extension and ankle plantar flexion moments with  
309 increasing cadence ( $p < 0.01$ ). The plantar flexion ankle moments were considerably lower (30-  
310 50%) than the hip and knee joint moments. Predictably, due to the increased crank angular velocity,  
311 there was a systematic increase in joint angular velocities with increasing cadence (Figure 2b).  
312 There was not a significant difference in peak knee positive powers across conditions (Figure 2c).

313

314 Predictably, we observed significantly greater positive work per cycle at slower cadences for all  
315 joints, however the distribution of joint positive work between the hip, knee, and ankle remained  
316 similar across cadences (Figure 3). For the knee joint, positive work was significantly greater for  
317 the 40 and 60 RPM conditions and significantly smaller for the 100 RPM condition compared to  
318 the preferred cadence. Collectively, total limb positive work per revolution significantly decreased  
319 with increasing cadence, whereas total limb negative work was not affected by cadence.

320

### 321 *Muscle mechanics*

322 The group mean ( $\pm$  SD)  $R^2$  value for the curve fits of the individual force-velocity curves was 0.78  
323  $\pm$  0.17 (11). The isokinetic experiments yielded estimates of peak VL fascicle power at  
324 approximately 25% of  $V_{\max}$  (1.2  $L_0/s$ ), of which only the 80 and 100 RPM conditions reached the

325 necessary shortening speed for peak power (Figure 4a). Peak VL fascicle efficiency was estimated  
326 to occur at 19% of  $V_{\max}$  ( $0.96 L_0/s$ ), which was closer to the peak shortening velocities of the 40  
327 RPM condition. There was a significant main effect of cadence on the power capacity during the  
328 period of positive power generation ( $p < 0.01$ ). The mean power capacity increased to a maximum  
329 at 80 RPM with significantly lower average power capacity at 40 RPM (Figure 4b). Cadence also  
330 had a significant main effect on the mean efficiency capacity, ranging from  $0.19 \pm 0.06$  at 40 RPM  
331 to  $0.21 \pm 0.05$  at 80 RPM.

332

### 333 *Activation*

334 The effect of cadence on peak muscle activation was variable across muscles. There were no  
335 significant effects of cadence on the peak activation of VL, RF, SOL, or BF; while MG did show  
336 a significant increase in peak activation as cadence increased ( $p < 0.01$ ). Thus, there was not a  
337 consistent pattern across all muscles or muscles within the same group for peak EMG to increase  
338 or decrease with cadence. When accounting for the different duration and number of revolutions  
339 for each cadence condition, there was a statistically significant increase in cumulative activation  
340 for all muscles (Figure 5a,b,  $p < 0.01$ ). When combined, there was also a significant effect of  
341 cadence on the total cumulative muscle activation of all muscles ( $p < 0.01$ ). The total cumulative  
342 muscle activation for all muscles showed a similar pattern to net metabolic power (Figure 5c) with  
343 lower overall activation at slower cadences.

344

### 345 **Discussion**

346 This study examined the effect of cycling cadence on VL fascicle mechanics, joint mechanical  
347 work, muscle activation, and whole-body metabolic cost during seated cycling. The data presented



348 provides a unique insight into determining how muscle fascicle mechanics relates to muscle  
349 energetics during cycling. Our data demonstrates that cadence did not alter the ratio of work  
350 production across different joints. Contrary to our hypothesis, VL efficiency (based on VL fascicle  
351 shortening velocity) was favourable for both the most economical cadence and preferred cadence.  
352 However, the preferred cadence had shortening velocities that were most favourable for the power  
353 generating capacity of VL. The total muscle activation per unit time was reduced at the most  
354 economical cadence which is consistent with the findings of Marsh and Martin (1995) (8). This  
355 work demonstrates the mechanisms that allow humans to be more economical at a cycling cadence  
356 that is lower than they would naturally prefer to pedal. The results also suggest that the preferred  
357 cadence is more favourable for the muscle power capacity of major work producing muscles, such  
358 as VL.

359

#### 360 *Joint work contributions to cycling energetics*

361 Cycling at different cadences at a constant submaximal power output resulted in consistent changes  
362 in joint work requirements and joint velocity across conditions. Forward dynamic simulations  
363 show the distribution of work between the hip, knee and ankle is a mechanical requirement to  
364 produce the energy to accelerate the crank (26,27). The uniarticular hip (gluteus maximus) and  
365 knee extensors (VL) generate the majority of the work to accelerate the crank, while the ankle  
366 plantar flexors (MG and SOL) transfer energy from the proximal muscles to the crank. Since the  
367 joint angular velocities are constrained by the crank velocity, there is a consistent distribution of  
368 joint work across cadence conditions (28). In this data, the knee and hip were the major  
369 contributors of positive work, as would be expected for seated cycling at submaximal intensities  
370 (29), with the knee performing approximately 70% of the total joint work per cycle. Importantly,

371 there was no significant change in the distribution of positive work between the joints across  
372 cadence: the participants increased the total work as required but did not shift the proportions of  
373 work from one joint to another. An alternative strategy could have been to shift a portion of the  
374 total work from the knee to the hip or ankle as cadence changed. It appears that the pedalling  
375 strategy is constrained by the requirement to produce energy to accelerate the crank (26,27). While  
376 the total amount of work performed by each joint in a single revolution decreases with increased  
377 cadence, the total net work performed over time should remain similar. Therefore, changes in joint  
378 work contributions are unlikely to contribute to changes in metabolic cost at different cadences.

379

380 *Knee joint kinetics, fascicle dynamics and the relationship to muscle activation and cycling*  
381 *energetics*

382 The changes in joint moments and mechanical work across cadence conditions indicate changes  
383 in muscle force and work production across cadence conditions. The greater knee joint moments  
384 and positive work at slow cadences must be produced by the quadriceps muscles, of which VL  
385 constitutes approximately 40% of the total physiological cross sectional area (25), and requires  
386 shortening of the muscle as the knee extends during the downstroke. We have previously shown,  
387 using this same data, that fascicle shortening and shortening velocity is significantly impacted by  
388 cadence and that there is a non-linear change in the VL fascicle shortening velocity with increased  
389 cadence, due to the involvement of the series elastic structure in absorbing and generating energy  
390 (11).

391

392 Here we have estimated the effect that the different VL fascicle velocities would have on muscle  
393 power and efficiency. Based on data collected using isokinetic contractions and a model of

394 energetics, we estimated peak efficiency to be 19% of maximum shortening velocity ( $V_{\max}$ )  
395 compared to peak power at 25%  $V_{\max}$ . The average fascicle shortening velocity resulted in the  
396 highest average VL power capacity occurring at 80 RPM, while the power capacity was  
397 significantly reduced at 40 RPM. The peak instantaneous fascicle shortening velocities when  
398 cycling at the slowest cadence (40 RPM) did not reach the peak of the power curve, occurring  
399 entirely on the ascending section. Therefore, pedalling at slower cadences results in VL fascicle  
400 shortening velocities that are less suitable for the power capacity of the muscle. However, the  
401 velocities of shortening at the preferred and most economical cadences resulted in similar overall  
402 VL efficiency estimates. As such, changes in VL fascicle velocity across a cycle are unlikely to  
403 explain the decreased metabolic cost at 60 RPM versus preferred.

404

405 The nervous system must activate muscles based on the force requirements of the movement and  
406 the functional capacity of the muscle to produce those forces. This ultimately affects metabolic  
407 cost, as muscles must activate/deactivate with varying magnitudes, rates, and durations. We did  
408 not observe consistent changes in EMG amplitude for all muscles across cadence conditions,  
409 which is most likely due to the concurrent changes in the force and velocity requirements of each  
410 muscle. For example, peak VL activation was not significantly affected by cadence, but the  
411 required forces are greater and fascicle shortening velocities lower at slow cadences compared to  
412 fast cadences. Thus, the VL force produced relative to the peak activation is greater at slow  
413 cadences compared to fast cadences, which coupled with the higher economy of low frequency  
414 contractions (30) may reduce the activation costs of force production at lower cadences (60 RPM).  
415 It is also possible that higher frequency contractions at higher cadence require faster motor units  
416 to achieve the required activation/deactivation rate (31,32), which might also incur a greater cost.

417

418 *Muscle activation and the most economical cadence*

419 The metabolic curve generated from the muscle activation data showed a curvilinear relationship,  
420 similar to that of previous data of comparable power outputs (33). There was a significantly greater  
421 metabolic cost to cycling at the preferred cadence ( $81 \pm 12$  RPM) compared to the most economical  
422 cadence of 60 RPM. Individual muscles exhibited different relationships between cadence and  
423 cumulative activation, making it difficult to identify specific muscles that might dominate changes  
424 in cumulative activation costs. Blake and Wakeling (2015) explored the effect of cadence and  
425 power output on efficiency (ratio of pedal power to total EMG intensity) and coordination,  
426 showing that the most efficient cadence (60 RPM at 100 W, 77 RPM at 200 W) is related to  
427 minimising total muscle excitation. Uniarticular muscles like VL and SOL showed consistent  
428 EMG intensity until the highest cadences (>120 RPM), whereas biarticular muscles like RF and  
429 MG exhibit greater changes in EMG intensity across lower cadences (40-120 RPM) (34). Our  
430 results differed in that both uni-articular (e.g. VL, SOL) and bi-articular muscles (e.g. RF, MG) in  
431 this study showed an increase in cumulative activation with cadence. This is most likely the result  
432 of representing EMG intensity per cycle compared to EMG per unit time, such that high cadences  
433 require a greater number of activation/deactivation cycles for a given distance/time. Our results  
434 primarily show that total cumulative activation is greater above the most economical cadence. Not  
435 only is there an increased number of activations for a given time period, but high frequency, short  
436 duration contractions have been shown to be less economical (30). Despite the increased force  
437 requirements, it appears to be beneficial in terms of activation cost and overall metabolic cost to  
438 cycle at slower cadences.

439

440 *The relationship between muscle work and power, and the preferred cycling cadence*

441 The preference for a particular cycling cadence, likely has a link to muscle contraction dynamics  
442 and the nervous system' knowledge of muscle performance parameters. Neptune and Hull (1999)  
443 argue, based on computer simulations, that the preferred cadence might minimise muscle force,  
444 stress and activation all major muscle groups are considered (7). Such simulations attempt to  
445 account for changes in muscle dynamics and how this influences their mechanical state and output,  
446 however the precise contractile conditions (e.g. fibre velocity and power output) were not explored  
447 in this study. Our results indicate that as cadence increased, there was an increase in VL fascicle  
448 shortening velocity and fascicle power capacity such that the mean power capacity was greatest at  
449 the preferred cadence and 80 RPM conditions. Thus, in cycling where there is a mechanical  
450 requirement for net positive power, a higher cadence than the most economic cadence is beneficial  
451 for producing VL muscle power. Therefore, it could be suggested that when the goal is to produce  
452 net positive power, a motor pattern that maximises the capacity for muscle power is utilised. At  
453 present, it is not clear how the nervous system would assess instantaneous muscle power relative  
454 to its maximal power capacity. Furthermore, a similar comment could be made regarding detection  
455 of metabolic rates relative to muscle mechanical energy for maximising movement efficiency.

456

457 One potential benefit of choosing a preferred cadence that favours muscle power is that it could  
458 provide a buffer against the steep ascending slope of the power and efficiency curves at low  
459 shortening velocities. If the shortening velocity of VL at the preferred cadence was concentrated  
460 at peak efficiency, and cadence was to decrease during the movement due to a sudden increase in  
461 power requirements (e.g. riding up a hill), the shortening velocity and subsequent power output  
462 from the muscle would reduce rapidly. Selecting a preferred cadence that results in shortening

463 velocities near peak power means that variations in cadence (and shortening velocity) would have  
464 limited effects on power and efficiency.

465

466 While the power capacity of VL appears to be maximised at the preferred cadence (near 80 RPM)  
467 for power output used this study (2.5W/kg or ~ 180W), a question remains as to whether the VL  
468 power output remains optimal with increased external power output requirements (33). At  
469 submaximal power outputs, as used in this study, positive power is primarily contributed by knee  
470 extension (28). However, as the overall external power requirements increase, there are greater  
471 relative contributions from hip extension and knee flexion power (29). This may suggest that  
472 power output of the knee may be limited by the requirement to shorten at high velocities and that  
473 power increases are mainly driven primarily by the hip. However, we have previously also shown  
474 that as cadence increases for a given power output, the reduction in knee extension moment allows  
475 the VL fascicle average shortening velocity to remain relatively constant (11), even though the  
476 MTU shortens at progressively higher rates. This is a consequence of the reduced requirement to  
477 stretch the elastic tissues due to lower forces being transmitted at higher cadence. Therefore,  
478 increasing cadence at higher power outputs reduces the required force with potentially little effect  
479 on the net fascicle shortening velocity; allowing the fascicles to still operate at near optimum  
480 velocity for generating maximum power. This hypothesis requires further experimental testing to  
481 confirm.

482

### 483 *Limitations*

484 There are a large number of muscles that actuate the hip, knee, and ankle joints in cycling, of which  
485 we have elected to observe changes in the largest of the quadriceps muscles. It is possible that

486 other muscles such as RF and BF are also significantly affected by cadence, however those muscles  
487 do not have the architecture that is suitable for the in vivo fascicle tracking method used in this  
488 study. As such, we elected to investigate a primary force producing muscle in cycling (VL) that  
489 allowed for measurement of in vivo fascicle mechanics. Furthermore, the position of the hip during  
490 the dynamometer task is not the same as the hip angle in cycling, since it is a dynamic multi-joint  
491 movement. The lengths of other muscles (RF, BF etc.) crossing the hip may therefore be affected  
492 by the chosen dynamometer hip angle.

493

494 We have used isokinetic maximum voluntary contractions to determine the relationship between  
495 force and velocity for VL. This has some potential limitations, particularly given that the highest  
496 achievable joint angular velocity was less than half that which would be required to achieve the  
497 true VL muscle-tendon unit  $V_{\max}$  (35). However, we have achieved similar force-velocity curves  
498 and estimations of  $V_{\max}$  to those already reported in the literature (35,36). The isokinetic data used  
499 to form the force-velocity curve in this study spans the range of shortening velocities at which  
500 peak power and efficiency was observed, as well as the cycling conditions. Therefore, the force-  
501 velocity curve has been measured up to the relevant shortening velocities to determine peak power  
502 and efficiency.

503

504 We have also based our estimates of efficiency off a model that assumes a linear relationship  
505 between shortening velocity and energy consumed by the muscle. The slope of this relationship  
506 may vary, which can influence the velocity that peak efficiency will occur. To inform the model  
507 we used parameters that match mammalian muscle (37) with properties intermediate to slow and  
508 fast twitch fibres. It is likely that higher cadences will require greater numbers of fast fibres, which

509 may further increase the velocity at which maximal efficiency occurs (13), however this is only  
510 likely to increase the efficiency value of the highest cadence, perhaps making efficiency based on  
511 velocity relatively flat across the cadence range.

512

### 513 **Conclusions**

514 These results support previous evidence that cyclists do not automatically select the most  
515 economical cadence, and instead prefer to use a higher cadence that has significantly greater  
516 metabolic cost. The most economical cadence appears to be the result of lower total cumulative  
517 muscle activation, and favourable VL shortening velocities for muscle efficiency, although the  
518 preferred cadence also had velocities favourable for high efficiency. There was no change in the  
519 proportion of work done at each joint that could account for differences in metabolic rate across  
520 cadence conditions. When pedalling at the preferred cadence, we observed fascicle shortening  
521 velocities that were favourable for muscle power capacity as well as efficiency. These results not  
522 only inform the mechanics and energetics of cycling but provide useful insight to the  
523 neuromuscular mechanism that might influence preferred movement patterns, particularly in tasks  
524 that require net positive power.

525

### 526 **Acknowledgments**

527 SF Brennan was supported by an Australian Postgraduate Award scholarship during the  
528 completion of this project. This project did not receive any external funding but did receive internal  
529 funding for the purchase of equipment.

530

531



532 **Conflict of Interest**

533 The authors have no conflicts of interest to declare with professionals, companies or manufacturers  
534 who may benefit from the results of the present study. The results of the present study do not  
535 constitute endorsement by ACSM. The results of the study are presented clearly, honestly, and  
536 without inappropriate data manipulation.

537 **References**

- 538 1. Holt KG, Hamill J, Andres RO. Predicting the minimal energy costs of human walking. *Med*  
539 *Sci Sports Exerc.* 1991 Apr;23(4):491–8.
- 540 2. Marsh AP, Martin PE. Effect of cycling experience, aerobic power, and power output on  
541 preferred and most economical cycling cadences. *Med Sci Sports Exerc.* 1997  
542 Sep;29(9):1225–32.
- 543 3. Ericson MO, Bratt A, Nisell R, Németh G, Ekholm J. Load moments about the hip and knee  
544 joints during ergometer cycling. *Scand J Rehabil Med.* 1986;18(4):165–72.
- 545 4. Ericson MO, Bratt Å, Nisell R, Arborelius UP, Ekholm J. Power output and work in different  
546 muscle groups during ergometer cycling. *Eur J Appl Physiol.* 1986 Jun;55(3):229–35.
- 547 5. Sawicki GS, Lewis CL, Ferris DP. It pays to have a spring in your step. *Exerc Sport Sci Rev.*  
548 2009 Jul;37(3):130–8.
- 549 6. Marsh AP, Martin PE, Sanderson DJ. Is a joint moment-based cost function associated with  
550 preferred cycling cadence? *J Biomech.* 2000 Feb;33(2):173–80.
- 551 7. Neptune RR, Hull ML. A theoretical analysis of preferred pedaling rate selection in endurance  
552 cycling. *J Biomech.* 1999 Apr;32(4):409–15.
- 553 8. Marsh AP, Martin PE. The relationship between cadence and lower extremity EMG in cyclists  
554 and noncyclists. *Med Sci Sports Exerc.* 1995 Feb;27(2):217–25.
- 555 9. Gordon AM, Huxley AF, Julian FJ. The variation in isometric tension with sarcomere length  
556 in vertebrate muscle fibres. *J Physiol-London.* 1966 May;184(1):170–92.
- 557 10. Hill AV. The heat of shortening and the dynamic constants of muscle. *P Roy Soc B-Biol Sci.*  
558 1938 Oct;126(843):136–95.

- 559 11. Brennan SF, Cresswell AG, Farris DJ, Lichtwark GA. The effect of muscle-tendon unit vs.  
560 fascicle analyses on vastus lateralis force-generating capacity during constant power output  
561 cycling with variable cadence. *J Appl Physiol*. 2018 Apr 1;124(4):993–1002.
- 562 12. Curtin N, Woledge R. Power at the expense of efficiency in contraction of white muscle fibres  
563 from dogfish *Scyliorhinus canicula*. *J Exp Biol*. 1996;199(3):593–601.
- 564 13. Barclay CJ. Efficiency of fast- and slow-twitch muscles of the mouse performing cyclic  
565 contractions. *J Exp Biol*. 1994 Aug;193:65–78.
- 566 14. Brennan SF, Cresswell AG, Farris DJ, Lichtwark GA. In vivo fascicle length measurements  
567 via B-mode ultrasound imaging with single vs dual transducer arrangements. *J Biomech*. 2017  
568 Nov;64:240–4.
- 569 15. Cronin NJ, Carty CP, Barrett RS, Lichtwark G. Automatic tracking of medial gastrocnemius  
570 fascicle length during human locomotion. *J Appl Physiol*. 2011 Nov;111(5):1491–6.
- 571 16. Farris DJ, Lichtwark GA. UltraTrack: Software for semi-automated tracking of muscle  
572 fascicles in sequences of B-mode ultrasound images. *Comput Methods Programs Biomed*.  
573 2016 May;128:111–8.
- 574 17. Delp SL, Anderson FC, Arnold AS, Loan P, Habib A, John CT, et al. OpenSim: open-source  
575 software to create and analyze dynamic simulations of movement. *IEEE Trans Biomed Eng*.  
576 2007 Nov;54(11):1940–50.
- 577 18. Azizi E, Roberts TJ. Muscle performance during frog jumping: influence of elasticity on  
578 muscle operating lengths. *Proc R Soc B*. 2010 May 22;277(1687):1523–30.
- 579 19. Curtin NA, Woledge RC. Power output and force-velocity relationship of live fibres from  
580 white myotomal muscle of the dogfish, *Scyliorhinus Canicula*. *J Exp Biol*. 1988;140:187–97.

- 581 20. Lichtwark GA, Wilson AM. A modified Hill muscle model that predicts muscle power output  
582 and efficiency during sinusoidal length changes. *J Exp Biol.* 2005 Aug;208(15):2831–43.
- 583 21. Nordeen-Snyder KS. The effect of bicycle seat height variation upon oxygen consumption  
584 and lower limb kinematics. *Med Sci Sports.* 1976;9(2):113–7.
- 585 22. Brockway JM. Derivation of formulae used to calculate energy expenditure in man. *Hum Nutr*  
586 *Clin Nutr.* 1987 Nov;41(6):463–71.
- 587 23. Delp SL, Loan JP, Hoy MG, Zajac FE, Topp EL, Rosen JM. An interactive graphics-based  
588 model of the lower extremity to study orthopaedic surgical procedures. *IEEE Trans Biomed*  
589 *Eng.* 1990;37(8):757–67.
- 590 24. Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G. Development of recommendations for  
591 SEMG sensors and sensor placement procedures. *J Electromyogr Kinesiol.* 2000 ed. 2000  
592 Oct;10(5):361–74.
- 593 25. Ward SR, Eng CM, Smallwood LH, Lieber RL. Are current measurements of lower extremity  
594 muscle architecture accurate? *Clin Orthop.* 2009 Apr;467(4):1074–82.
- 595 26. Neptune RR, Herzog W. Adaptation of muscle coordination to altered task mechanics during  
596 steady-state cycling. *J Biomech.* 2000 Feb;33(2):165–72.
- 597 27. Raasch CC, Zajac FE. Locomotor strategy for pedaling: muscle groups and biomechanical  
598 functions. *J Neurophysiol.* 1999 Aug 1;82(2):515–25.
- 599 28. Ericson MO. Mechanical muscular power output and work during ergometer cycling at  
600 different work loads and speeds. *Eur J Appl Physiol.* 1988;57(4):382–7.
- 601 29. Elmer SJ, Barratt PR, Korff T, Martin JC. Joint-specific power production during submaximal  
602 and maximal cycling. *Med Sci Sports Exerc.* 2011 Oct;43(10):1940–7.

- 603 30. Hogan MC, Ingham E, Kurdak SS. Contraction duration affects metabolic energy cost and  
604 fatigue in skeletal muscle. *Am J Physiol.* 1998 Mar;274(3):E397–402.
- 605 31. Blake OM, Wakeling JM. Early deactivation of slower muscle fibres at high movement  
606 frequencies. *J Exp Biol.* 2014 Oct 1;217(Pt 19):3528–34.
- 607 32. Wakeling JM, Uehli K, Rozitis AI. Muscle fibre recruitment can respond to the mechanics of  
608 the muscle contraction. *J R Soc Interface.* 2006 Feb 10;3(9):533–44.
- 609 33. Coast JR, Welch HG. Linear increase in optimal pedal rate with increased power output in  
610 cycle ergometry. *Eur J Appl Physiol.* 1985 Feb;53(4):339–42.
- 611 34. Blake OM, Wakeling JM. Muscle coordination limits efficiency and power output of human  
612 limb movement under a wide range of mechanical demands. *J Neurophysiol.* 2015  
613 Dec;114(6):3283–95.
- 614 35. Hauraix H, Dorel S, Rabita G, Guilhem G, Nordez A. Muscle fascicle shortening behaviour  
615 of vastus lateralis during a maximal force-velocity test. *Eur J Appl Physiol.* 2017  
616 Feb;117(2):289–99.
- 617 36. Fontana H de B, Roesler H, Herzog W. In vivo vastus lateralis force-velocity relationship at  
618 the fascicle and muscle tendon unit level. *J Electromyogr Kinesiol.* 2014 Dec;24(6):934–40.
- 619 37. Barclay CJ, Constable JK, Gibbs CL. Energetics of fast- and slow-twitch muscles of the  
620 mouse. *J Physiol-London.* 1993 Dec;472:61–80.

621

622

623 **Figure Legends**

624 Figure 1. Net metabolic power as a function of cadence. There was a significant effect of cadence  
625 on metabolic cost, with the minimum occurring at 60 RPM. The preferred cadence of 81 RPM  
626 recorded a significantly higher metabolic cost than 60 RPM and a significantly lower cost  
627 compared to 100 RPM. Data points means  $\pm$  standard deviation. Astricts (\*) show significant  
628 differences versus the preferred cadence.

629

630 Figure 2. Group mean waveforms for knee joint kinematics and kinetics. There was a knee  
631 extension moment (a) during the first half of the cycle that decreased with increasing cadence.  
632 Joint velocity (b) increased with cadence due to a faster crank angular velocity. (c) The knee joint  
633 exhibited two periods of positive power: a large positive power period during the down stroke,  
634 which coincides with the knee extension moment and a lesser period as the knee joint flexed during  
635 the upstroke. Different line types represent the different cadences. The mean preferred cadence  
636 condition is not shown as it closely resembles the 80 RPM condition. Error bars show  $\pm$  1 standard  
637 deviation for the preferred cadence condition.

638

639 Figure 3. Group mean positive work per revolution for each of the lower limb joints for the 40, 60,  
640 80, and 100 RPM conditions. The radius of each concentric circle is scaled to the summed positive  
641 work of all the joints and shows that as cadence increased, the amount of positive work per  
642 revolution decreased. The distribution of positive work across the three joints remained relatively  
643 constant. The knee provided the largest proportion of total limb work, followed by the hip and then  
644 ankle.

645

646 Figure 4. The effect of cadence on VL fascicle mechanics relative to the force-velocity relationship  
647 and estimated average power and efficiency. (a) As cycling cadence increased, peak VL shortening  
648 velocities were closer to the peak of the power curve (grey, dot-dash) compared to slower cadences  
649 that are closer to the peak of the efficiency curve (grey, dot). Vertical lines show the group mean  
650 peak shortening velocity for each cycling cadence. The curves shown are group means which  
651 demonstrate the shape of the relationship. (b) The power capacity was significantly different across  
652 cadence conditions with a peak at 80 RPM. The efficiency capacity (reported as a fraction of work  
653 output relative to predicted energetic cost) was significantly affected by cadence across conditions,  
654 with decreased efficiency at 40 RPM. Data are shown as mean  $\pm$  standard deviation. Grey symbols  
655 show the preferred cadence.

656

657 Figure 5. Muscle activation of four lower limb muscles at each cadence. There was an increase in  
658 cumulative activation with cadence for the (a) quadriceps (VL, RF) and (b) plantar flexor (MG,  
659 SOL) muscles, which generally increased as cadence increased. (c) There was a curvilinear  
660 increase in the total cumulative activation with greater overall activation as cadence increased (left  
661 axis). Total activation represents the sum of the mass relative, cumulative muscle activations of  
662 the VL, RF, BF, MG and SOL muscles. Biceps femoris was omitted from for clarity. Error bars  
663 show the standard deviation.

664