



Exercise tolerance during muscle contractions below and above the critical torque in different muscle groups

Journal:	<i>Applied Physiology, Nutrition, and Metabolism</i>
Manuscript ID	apnm-2017-0381.R2
Manuscript Type:	Article
Date Submitted by the Author:	24-Sep-2017
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Is the invited manuscript for consideration in a Special Issue? :	
Keyword:	exercise, isometric, maximal voluntary contraction, fatigue, exercise intensity domain

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Abstract

The objective of this study was to test the hypotheses that end-test torque (ET) (expressed as % maximal voluntary contraction - MVC) is higher for plantar flexors (PF) than knee extensors (KE) muscles, whereas impulse above ET (IET) is higher for KE than PF. Thus, we expected that exercise tolerance would be longer for KE than PF only during the exercise performed above ET. After the determination of MVC, forty men performed two 5-min all-out tests to determine ET and IET. Eleven participants performed a further four intermittent isometric tests, to exhaustion, at ET + 5% and ET - 5%, and one test for KE at the exercise intensity (%MVC) corresponding to ET + 5% of PF. The IET (7243.2 ± 1942.9 vs. 3357.4 ± 1132.3 Nm·s) and ET (84.4 ± 24.8 vs. 73.9 ± 19.5 N·m) were significantly lower in PF compared with KE, respectively. The exercise tolerance was significantly longer for PF (300.7 ± 156.7 s) than KE (156.7 ± 104.3 s) at similar %MVC (~ 60%), and significantly shorter for PF (300.7 ± 156.7 s) than KE (697.0 ± 243.7 s) at ET + 5% condition. However, no significant difference was observed for ET - 5% condition (KE = 1030.2 ± 495.4 s vs. PF = 1028.3 ± 514.4 s). Thus, the limit of tolerance during submaximal isometric contractions is influenced by absolute MVC only during exercise performed above ET, which seems to be explained by differences on both ET (expressed as %MVC) and IET values.

Key words: maximal voluntary contraction, exercise, isometric, muscle volume, fatigue, exercise intensity domain.

37

38 Introduction

39 Exercise tolerance during different high intensity exercise protocols (i.e.,
40 constant work rate, incremental, self-paced and all-out) can be predicted by a
41 hyperbolic work rate/time function (i.e., critical power model) (Chidnok et al.
42 2013; Souza et al. 2015). Using this function, it is possible to estimate both the
43 critical power (the asymptote of the power/time hyperbola) and the hyperbola's
44 curvature constant (W') (Dekerle et al. 2015). Critical power has been considered
45 the lower boundary of severe intensity domain and corresponds to the highest
46 sustainable rate of oxidative metabolism. The W' represents the total amount of
47 work that can be performed above critical power before exhaustion occurs.
48 Traditionally, critical power and W' and those equivalent for running and
49 swimming (critical velocity and D' , respectively), have been estimated by 3-5
50 high-intensity constant work-rate exercises (Jones et al. 2010). Aiming to reduce
51 the number of bouts of exhaustive exercise, Vanhatalo et al. (2007)
52 demonstrated that the parameters of critical power model can be estimated by a
53 single 3-min all-out exercise test. In this protocol, the end-test power (the power
54 output in the last 30 s of the test) and the work done above end-test power were
55 similar to the parameters (critical power and W' , respectively) estimated during
56 the conventional protocol (i.e., constant work-rate exercises).

57 Recently, some studies have utilized 5-min all-out intermittent isometric
58 single-leg knee-extensor exercise to characterize muscle bioenergetics and
59 fatigue (Burnley et al. 2012; Broxterman et al. 2017). Moreover, this protocol has
60 been utilized to estimate the critical force / torque during exercise involving

61 different muscle groups (e.g., knee extensors and forearm flexors) (Burnley 2009;
62 Kellawan and Tschakovsky 2014). Interestingly, the intramuscular metabolic
63 response and the torque vs. time shape curve are similar to that observed during
64 the 3-min all-out cycling exercise (Burnley et al. 2012; Broxterman et al. 2017).
65 Indeed, Burnley (2009) verified that the end-test torque (ET) during 5-min all-out
66 knee extensor protocol is similar to the asymptote of the torque-duration
67 relationship (i.e., critical torque). In line with this data, Kellawan and Tschakovsky
68 (2014) have shown that the parameters estimated during this protocol presented
69 an excellent repeatability (ET, ICC = 0.94) and are valid to predict the exercise
70 tolerance during exercise at a constant intensity above the ET.

71 Submaximal isometric contraction (sustained or repeated) performed at a
72 given % of an individual's maximum voluntary contraction (%MVC) has been
73 extensively utilized to normalize the exercise intensity during different
74 experimental designs and clinical settings (Frey Law et al. 2010; Millar et al.
75 2014). This paradigm assumes that both acute and chronic physiological
76 responses to submaximal isometric contraction present a low inter individual
77 variability. In addition, %MVC has also been utilized to compare acute response
78 to submaximal isometric contraction involving different muscle groups. However,
79 exercise tolerance during submaximal isometric contraction presents a high inter
80 individual variability (Frey Law et al. 2010) and is proposed to be dependent on
81 absolute force/muscle cross-sectional area (Hunter and Enoka 2001). Higher
82 absolute force during isometric contraction is associated with partial occlusion of
83 blood flow and impairment of oxygen delivery to the muscle. The O₂ delivery is

84 an important determinant of critical torque / force, and presumably, the exercise
85 tolerance during submaximal isometric contraction (Kellawan et al. 2014).
86 Notwithstanding, a greater absolute force/muscle cross-sectional area could be
87 associated with higher impulse accumulated above critical torque (IET) (Byrd et
88 al. 2017). In the critical torque model, IET is only utilized during exercise
89 performed above critical torque, and task failure at this intensity is associated
90 with its complete utilization (Dekerle et al. 2015). Thus, exercise tolerance during
91 submaximal isometric contraction would be better analysed using the critical
92 torque model, instead a given %MVC.

93 To date, the parameters of critical torque model obtained in muscle groups
94 with different absolute MVC values and their possible influence on exercise
95 tolerance has not been assessed within distinct exercise intensity domains. Thus,
96 the main objectives of this study were: a) to compare the parameters estimated
97 by the critical torque model between the knee extensors (KE) and plantar flexors
98 (PF) muscle groups; and b) to compare the exercise tolerance of the KE and PF
99 muscle groups during the exercise performed bellow ($- 5\%$) and above ($+ 5\%$)
100 ET. We hypothesized that: 1) the PF would present a higher ET (expressed as
101 %MVC) than KE; 2) the KE would present a higher IET than PF; 3) the exercise
102 tolerance during the exercise performed above ET (i.e., severe exercise domain)
103 will be higher for KE than PF, and; 4) the exercise tolerance will be similar
104 between PF and KE muscle groups during the exercise performed bellow ET.

105

106 **Methods**

107 Subjects

108 Forty active males (mean \pm SD, 25.5 \pm 5.0 years; 75.7 \pm 15.0 kg; 175.5 \pm
109 6.5 cm) volunteered to participate in the study. All participants were healthy and
110 free of cardiovascular, respiratory, and neuromuscular diseases. All risks
111 associated with the experimental procedures were explained before involvement
112 in the study and each participant signed an informed consent form. The study
113 was performed based on the Declaration of Helsinki, and the protocol was
114 approved by the University's Ethics Committee.

115

116 Experimental design

117 The participants were tested in a climate-controlled (21–23°C) laboratory
118 at the same time of day (\pm 2 h) to minimize the effects of diurnal biological
119 variation. In the first visit, each participant performed a familiarization session to
120 the isokinetic dynamometer. On the following two visits, the participants
121 performed maximal isometric voluntary contractions (MVC) of the KE and PF to
122 determine isometric peak torque. After 30 min of rest, the participants performed
123 a 5-min intermittent all-out test, to determine the ET and IET. The order of the
124 two experimental sessions was randomized. Eleven participants performed a
125 further five intermittent tests, to exhaustion, at different intensities, to determine
126 the time limit. These tests were conducted at different days and the order of the
127 intensities was randomized within the same muscle group. The interval between
128 the experimental sessions was at least 48 h. The participants were instructed to
129 arrive at the laboratory in a rested and fully hydrated state at least 3 h post-

130 prandial, and they were asked not to perform any strenuous activity during the
131 day prior to each test.

132

133 **Familiarization**

134 Familiarization involved maximal (5 min) and submaximal (10 min)
135 isometric voluntary contractions with 3-s duration, interspersed with 2 s of rest.
136 For the submaximal contractions the target torque was displayed on a screen.

137

138 **Maximal voluntary contraction**

139 For KE muscles, participants were placed in a sitting position and securely
140 strapped into the test chair, with the hip and knee joints at angles of 85° and 75°,
141 respectively. The joint angles were measured using a goniometer. Extraneous
142 movement of the upper body was limited by two cross-shoulder harnesses and
143 an abdomen belt. The axis of the dynamometer was aligned with the right knee
144 flexion-extension axis, and the lever arm was attached to the participant's shank
145 with a strap. For PF muscles, the participants lay supine on the seat of the
146 dynamometer, with hip at 25° of flexion and the knee at full extension (0°) and
147 knee angles, and the ankle angle at 90°. The joint angles were measured using a
148 goniometer. Extraneous movement of the upper body was limited by two cross-
149 shoulder harnesses, and straps at the waist, the thigh, the shank and the foot.
150 The chair settings were recorded and replicated in all tests. Participants were
151 asked to relax their leg so that the effects of gravity on the passive limb and lever
152 arm could be measured. The warm-up of the isometric tests consisted of a set of

153 five submaximal isometric contractions, followed by 5-min rest. The peak torque
154 measurement involved three isometric MVC of 3 s, separated by a rest period of
155 3 minutes. The test was performed in the dominant limb. The participants were
156 instructed to perform a maximum effort for each trial, and strong verbal
157 encouragement was provided by the researchers. The peak torque corresponded
158 to the highest torque value attained during the trials.

159

160 **End-test torque and impulse above end-test torque**

161 A 5-min all out test was utilized to determine ET and IET of KE and PF. It
162 consisted of 60 maximal intermittent isometric contractions (3 s exercise, 2 s rest)
163 (Burnley 2009). Before the test, a 10-min warm-up was given, consisting of
164 submaximal isometric contractions and MVC, followed by 5-min rest before the
165 commencement of the test. The participants were informed about their MVC
166 value measured during the warm-up period, and instructed to attain or exceed
167 this value during the first 3-5 contractions of the test. During the whole test, they
168 were strongly encouraged to perform the maximal effort at each muscle
169 contraction, but not received information regarding the elapsed time and
170 contractions remaining. The ET corresponded to the mean torque values of the
171 last six contractions, and IET was estimated through to the area under the torque
172 vs. time curve (Burnley 2009).

173

174 **Submaximal trials**

175 The constant-load intermittent tests to exhaustion were performed at ET +
176 5% and ET - 5% for both muscle groups, in random order. Additionally, another
177 constant-load intermittent test to exhaustion was performed for KE muscle
178 groups at the exercise intensity (i.e., %MVC) corresponding to the ET + 5% of
179 the PF muscle group. During these tests, the individuals performed submaximal
180 isometric contractions of 3 s interspersed with 2 s of recovery until task failure.
181 The target torque was shown in the computer display screen with a red line. The
182 participants were verbally encouraged to maintain the target torque in all
183 contractions. The time of the first of three consecutive muscle contractions where
184 the subject was unable to attain the target torque even with verbal
185 encouragement corresponded to the time limit (Burnley 2009; Kellawan and
186 Tschakovsky 2014) (Figure 1).

187

188 **Measurements**

189 The torque data were sampled at 1000 Hz (Miotec®, Porto Alegre/RS,
190 Brasil) and were analyzed using algorithms written in Matlab (The MathWorks,
191 Natick, MA, USA). The torque curves were smoothed by a digital fourth-order
192 zero-lag Butterworth filter with a cutoff frequency of 20 Hz (Winter, 1990).

193

194 **Statistical analysis**

195 The data are presented as means \pm SD. The normality of data was
196 checked by the Shapiro-Wilk test. A Student *t* test for paired data was used to
197 compare the variables MVC, ET, IET and time limit between the muscle groups.

198 The relationship between the time limit predicted from the critical power model
199 and actual time limit was assessed using Pearson's product moment correlation
200 coefficient. The significance level was set at $p < 0.05$ and effect sizes (ES) were
201 calculated.

202

203 **Results**

204 **MVC and parameters of critical torque model**

205 The mean \pm SD values of MVC, IET, and ET for KE and PF are shown in
206 Table 1. The MVC (ES = 2.19), IET (ES = 2.44) and ET (ES = 0.47) were
207 significantly lower in PF compared with KE ($p < 0.01$). However, the ET
208 expressed as a percentage of MVC was significantly higher in PF ($40.9 \pm 7.7\%$
209 MVC) than KE ($29.0 \pm 8.1\%$ MVC) ($p < 0.01$; ES = 1.50). The IET/MVC was
210 significantly smaller for PF compared with KE (PF = 17.7 ± 5.4 vs. KE = $22.4 \pm$
211 7.9 , ES = 1.25). However, the ET/MVC was significantly greater for PF compared
212 with KE (PF = 0.41 ± 0.08 vs. 0.29 ± 0.08 , ES = 1.50). The mean torque profile of
213 the 5-min test is shown in Figure 2.

214 There was significant correlation between IET and MVC for both KE ($r =$
215 0.67 , $p < 0.05$) and PF ($r = 0.62$, $p < 0.05$) muscle groups. However, the
216 correlation between ET and MVC was significant only for PF ($r = 0.71$, $p < 0.05$).

217

218 **Exercise tolerance**

219 The actual torque values performed during the exercise tolerance tests
220 were 116 ± 15 N·m and 106 ± 14 N·m for ET + 5% and ET - 5%, respectively.

221 The actual torque performed during the exercise condition at the exercise
222 intensity (i.e., %MVC) corresponding to the ET + 5% of the PF was 178.8 ± 34.8
223 N·m, and corresponded to $59 \pm 8\%$ MVC.

224 The mean \pm SD values of the time limit obtained during the time
225 exhaustion tests at ET + 5%, ET - 5% and %MVC are presented in Table 2.
226 There was no significant difference between actual and predicted time limit for
227 KE and PF at ET + 5% condition. Additionally, significant correlation between the
228 actual and predicted time limit for both KE ($r = 0.66$) and PF ($r = 0.72$) was
229 observed. The time limit at ET + 5% was significantly shorter for PF than KE ($p <$
230 0.001 , ES = 1.93). However, the time limit of KE and PF was similar at ET - 5%
231 condition ($p = 0.45$, ES = 0.01), but it was significantly longer for PF than KE at
232 %MVC condition ($p < 0.001$, ES = 1.08).

233

234 Discussion

235 The main objectives of this study were to compare both the parameters
236 estimated by the critical torque model and the exercise tolerance during exercise
237 performed bellow and above ET in muscle groups with different MVC values (i.e.,
238 KE vs. PF). Consistent with previous research (Hunter and Enoka 2001), it was
239 verified that exercise tolerance is dependent on absolute force (i.e., PF > KE)
240 during severe-intensity exercise performed at similar %MVC (~ 60%). However,
241 the main and original findings were as follows: (1) exercise tolerance is
242 dependent on IET (i.e., KE > PF) when submaximal isometric contraction is
243 performed at similar amplitude (5%) above ET; (2) exercise tolerance is

244 independent on absolute force when submaximal isometric contraction is
245 performed at similar amplitude (5%) below ET; and (3) MVC explain, at least in
246 part, both the inter individual variability and the difference observed in ET and
247 IET of KE and PF. The main implication of these findings is that absolute MVC
248 influences exercise tolerance during submaximal isometric contractions only
249 when ET is exceeded.

250

251 **Validity of 5-min all-out intermittent isometric**

252 There is a substantial body of evidence indicating that a single 3-min all-
253 out cycling test against fixed resistance is valid to estimate the parameters of
254 critical power model (critical power and W') determined during conventional
255 protocol (i.e., constant work-rate exercises) (Vanhatalo et al. 2007; Vanhatalo et
256 al. 2008). During this protocol, the finite work capacity is continuous utilized, such
257 that the work done above EP is similar to W' and the power output plateau at
258 critical power. Interestingly, the skeletal muscle bioenergetics (i.e., sources and
259 rates of ATP synthesis) and the magnitudes of intramuscular metabolic
260 perturbation (e.g., pH and $[P_i]$) during 3-min all-out cycling exercise and 5-min all-
261 out intermittent isometric exercise seems to be very similar (Broxterman et al.
262 2017). Thus, all-out intermittent isometric protocols seem to be an attractive
263 approach to investigate the physiological response during a single test.

264 Few studies have analysed the validity of 5-min all-out intermittent
265 isometric exercise to estimate the parameters determined during the critical
266 torque / force model. Burnley (2009) verified that ET obtained during repeated

267 maximal isometric contractions of the KE was not different and significant
268 correlated ($r = 0.88$, $p = 0.004$) with critical torque estimated from the impulse-
269 time model. Using a different approach and muscle group (i.e., forearm flexors),
270 Kellawan and Tschakovsky (2014) verified that the 5-min all-out intermittent
271 isometric exercise is valid to estimate the parameters of critical torque model. In
272 this study, time limit predicted by ET and IET showed a good agreement with
273 actual time limit during exercise at a constant intensity above the ET ($r = 0.97$, p
274 < 0.01). The data of the present study confirm and extend the validity of the 5-
275 min all-out intermittent isometric protocol, since the actual time was not different
276 and significantly correlated with time limit predicted by ET and IET, irrespectively
277 of muscle group.

278

279 **Exercise tolerance across exercise intensity domains and muscle groups**

280 Traditionally, a given %MVC has been utilized to analyse the limit of
281 tolerance during small-muscle-mass exercise (Frey Law et al. 2010). In this
282 model, exercise tolerance has been inversely related with absolute force/muscle
283 cross-sectional area (Hunter and Enoka 2001). Indeed, the present study found
284 that exercise tolerance during similar repeated submaximal isometric
285 contractions (i.e., ~ 60 %MVC) was significantly longer for PF than for KE.
286 Differences in blood flow occlusion and impairment of oxygen delivery to the
287 muscle has been claimed as an important mechanism to explain the effect of
288 absolute force/muscle cross-sectional area on exercise tolerance (Hunter and
289 Enoka 2001). However, a different scenario emerges when the critical torque

290 model was utilized to compare the limit of tolerance between KE and PF. During
291 repeated submaximal isometric contractions performed above ET (i.e., ET + 5%),
292 KE presented a longer exercise tolerance than PF. Exercise tolerance during
293 exercise performed above critical torque is influenced by both the magnitude of
294 IET and the rate of its utilization (i.e., the exercise intensity amplitude above ET)
295 (Dekerle et al. 2015). Indeed, different experimental design has confirmed that
296 the size of the W' remains constant irrespective of its rate of expenditure, with
297 task failure coinciding with consistently low values of muscle PCr and pH, and
298 accumulation of fatigue-related metabolites (i.e., Pi, H⁺) (Vanhatalo et al. 2010).
299 Thus, the higher magnitude of IET seems to explain the longer exercise tolerance
300 of KE during exercise performed at similar amplitude above ET (i.e., > 5%). A
301 different condition is presented when KE and PF were compared during similar
302 repeated submaximal isometric contractions (i.e., ~ 60 %MVC). In this condition,
303 KE performed the exercise at higher amplitude in relation to ET (KE = ET + 60%
304 vs. PF = ET + 5%), and consequently, its higher magnitude of IET is not sufficient
305 to determine similar time limit. Finally, exercise performed below ET is
306 characterized by stable values for [PCr], [Pi], and pH with no substantial
307 utilization of W' (Jones et al. 2008). Thus, exercise tolerance at this intensity is
308 theoretically independent of IET magnitude. Indeed, time limit was not
309 significantly different between KE and PF. The mechanism responsible for
310 muscle fatigue during this exercise intensity is apparently more complex, and
311 seems to be linked with both metabolic and ionic perturbation (Black et al. 2017).
312

313 **MVC and parameters of critical torque model**

314 Few studies have investigated the possible influence of neuromuscular
315 characteristics on the parameters estimated from the critical power model. The
316 present study verified that inter individual variability of IET was moderated
317 explained by MVC. Moreover, both MVC and IET were significantly higher for KE
318 than for PF, although IET normalized by MVC was different between muscles
319 groups. The muscle volume, an important determinant of MVC, would explain the
320 influence of absolute force on IET. Hypothetically, a greater muscle volume could
321 be associated with elevated stored energy sources ([PCr], [ATP], glycogen, and
322 oxygen bound to myoglobin) and consequently, a higher IET. Indeed, during
323 whole-body exercise, Miura et al. (2002) showed a positive correlation ($r = 0.59$,
324 $p < 0.01$) between W' and muscle cross sectional area of the thigh. In line with
325 this data, Byrd et al. (2017) verified that local mineral-free thigh lean mass was
326 significantly related with W' determined during cycle exercise. However, there is
327 no study that has investigated the influence of muscle volume on IET. Thus,
328 future studies should investigate the influence of neuromuscular characteristics
329 (e.g., muscle volume, muscle fibre type) on IET during small-muscle-mass
330 exercise.

331 Several lines of evidence indicate that critical power / ET is aerobic in
332 nature, and consequently, influenced by oxygen delivery to the muscle (Kellawan
333 et al. 2014). The ET expressed as absolute values was significantly higher for KE
334 than for PF. However, ET expressed as relative values and normalized by MVC
335 was significantly higher for PF than for KE. A smaller muscle force/volume has

336 been associated with lower blood pressure during isometric contractions,
337 allowing increased blood flow and oxygen delivery to the muscle. Moreover,
338 during whole-body exercise, it has been verified that critical power was correlated
339 with muscle type I ($r = 0.67$, $p = 0.025$) and inversely correlated with muscle type
340 IIx fibre proportion ($r = -0.76$, $p = 0.01$) (Vanhatalo et al. 2016). Thus, difference
341 in blood flow and muscle type I distribution could explain, at least in part, a higher
342 ET expressed as relative values for PF.

343 Finally, we acknowledge the potential limitation of using a single joint
344 angle to compare MVC and exercise tolerance during small-muscle-mass
345 exercise. The joint angle influences both MVC and exercise tolerance during
346 submaximal isometric contraction (Boyas and Guével 2011), and consequently,
347 the effects of muscle group on ET and IET could be muscle length dependent.

348

349 **Conclusion**

350 In summary, this study has demonstrated that during repeated submaximal
351 isometric contractions performed at similar %MVC, exercise tolerance seems to
352 be negatively influenced by absolute force. Above similar amplitude of ET,
353 exercise tolerance is positively influenced by IET, which is partially explained by
354 MVC, independently of muscle group. However, limit of tolerance during
355 submaximal isometric contractions performed below ET is independent of IET.
356 Thus, the limit of tolerance during small-muscle-mass exercise is influenced by
357 absolute MVC only during exercise performed above ET, which seems to be
358 explained by differences on both ET (expressed as %MVC) and IET values.

359

360 Conflict of interest

361 The authors report no conflicts of interest associated with this manuscript.

362

363 **References**

364 Abe, T., Kondo, M., Kawakami, Y., and Fukunaga, T. 1994. Prediction equations
365 for body composition of Japanese adults by B-mode ultrasound. *Am. J. Hum.*
366 *Biol.* **6**(2): 161-170. doi: 10.1002/ajhb.1310060204.

367 Black, M.I., Jones, A.M., Blackwell, J.R., Bailey, S.J., Wylie, L.J., McDonagh,
368 S.T., Thompson, C., Kelly, J., Sumners, P., Mileva, K.N., Bowtell, J.L., and
369 Vanhatalo, A. 2017. Muscle metabolic and neuromuscular determinants of
370 fatigue during cycling in different exercise intensity domains. *J. Appl. Physiol.*
371 **122**(3): 446-459. doi: 10.1152/jappphysiol.00942.2016.

372 Boyas, S., and Guével. A. 2011. Influence of exercise intensity and joint angle on
373 endurance time prediction of sustained submaximal isometric knee extensions.
374 *Eur. J. Appl. Physiol.* **111**(6): 1187-1196. doi: 10.1007/s00421-010-1731-0.

375 Broxterman, R.M., Layec, G., Hureau, T.J., Amann, M., and Richardson, R.S.
376 2017. Skeletal muscle bioenergetics during all-out exercise: mechanistic insight
377 into the oxygen uptake slow component and neuromuscular fatigue. *J. Appl.*
378 *Physiol.* **122**(5): 1208-1217. doi: 10.1152/jappphysiol.01093.2016.

379 Burnley, M., Vanhatalo, A., and Jones, A.M. 2012. Distinct profiles of
380 neuromuscular fatigue during muscle contractions below and above the critical

- 381 torque in humans. *J. Appl. Physiol.* **113**(2): 215-223. doi:
382 10.1152/jappphysiol.00022.2012.
- 383 Burnley, M. 2009. Estimation of critical torque using intermittent isometric
384 maximal voluntary contractions of the quadriceps in humans. *J. Appl. Physiol.*
385 **106**(3): 975-983. doi: 10.1152/jappphysiol.91474.2008.
- 386 Byrd, M.T., Switalla, J.R., Eastman, J.E., Wallace, B.J., Clasey, J.L., and
387 Bergstrom, H.C. 2017. Contributions of body composition characteristics to
388 critical power and anaerobic work capacity. *Int. J. Sports Physiol. Perform.* **22**:1-
389 20. doi: 10.1123/ijsp.2016-0810.
- 390 Chidnok, W., Dimenna, F.J., Bailey, S.J., Wilkerson, D.P., Vanhatalo, A., and
391 Jones, A.M. 2013. Effects of pacing strategy on work done above critical power
392 during high-intensity exercise. *Med. Sci. Sports Exerc.* **45**(7): 1377-1385. doi:
393 10.1249/MSS.0b013e3182860325.
- 394 Dekerle, J., de Souza, K.M., de Lucas, R.D., Guglielmo, L.G., Greco, C.C., and
395 Denadai, B.S. 2015. Exercise Tolerance Can Be Enhanced through a Change in
396 Work Rate within the Severe Intensity Domain: Work above Critical Power Is Not
397 Constant. *PLoS One* **10**(9): e0138428. doi: 10.1371/journal.pone.0138428.
- 398 Frey Law, L.A., and Avin, K.G. 2010. Endurance time is joint-specific: a modelling
399 and meta-analysis investigation. *Ergonomics* **53**(1): 109-129. doi:
400 10.1080/00140130903389068.
- 401 Hunter, S.K., and Enoka, R.M. 2001. Sex differences in the fatigability of arm
402 muscles depends on absolute force during isometric contractions. *J. Appl.*
403 *Physiol.* **91**(6): 2686-2694.

- 404 Ishida, Y., Kanehisa, H., Carroll, J.F., Pollock, M.L., Graves, J.E., and Leggett,
405 S.H. 1995. Body fat and muscle thickness distributions in untrained young
406 females. *Med. Sci. Sports Exerc.* **27**(2): 270–274.
- 407 Jones, A.M., Vanhatalo, A., Burnley, M., Morton, R.H., and Poole, D.C. 2010.
408 Critical power: implications for determination of VO_2max and exercise tolerance.
409 *Med Sci Sports Exerc.* **42**(10): 1876-1890. doi: 10.1249/MSS.0b013e3181d9cf7f.
- 410 Jones, A.M., Wilkerson, D.P., DiMenna, F., Fulford, J., and Poole, D.C. 2008.
411 Muscle metabolic responses to exercise above and below the "critical power"
412 assessed using ^{31}P -MRS. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **294**(2):
413 R585-593.
- 414 Kellawan, J.M., Bentley, R.F., Bravo, M.F., Moynes, J.S., and Tschakovsky, M.E.
415 2014. Does oxygen delivery explain interindividual variation in forearm critical
416 impulse? *Physiol. Rep.* **2**(11) pii: e12203. doi: 10.14814/phy2.12203.
- 417 Kellawan, J.M., and Tschakovsky, M.E. 2014. The single-bout forearm critical
418 force test: a new method to establish forearm aerobic metabolic exercise
419 intensity and capacity. *PLoS One* **9**(4): e93481. doi:
420 10.1371/journal.pone.0093481.
- 421 Miyatani, M., Kanehisa, H., Ito, M., Kawakami, Y., and Fukunaga, T. 2004. The
422 accuracy of volume estimates using ultrasound muscle thickness measurements
423 in different muscle groups. *Eur. J. Appl. Physiol.* **91**(2-3): 264-272.
- 424 Millar, P.J., McGowan, C.L., Cornelissen, V.A., Araujo, C.G., and Swaine, I.L.
425 2014. Evidence for the role of isometric exercise training in reducing blood

- 426 pressure: potential mechanisms and future directions. *Sports Med.* **44**(3): 345-
427 356. doi: 10.1007/s40279-013-0118-x.
- 428 Miura, A., Endo, M., Sato, H., Sato, H., Barstow, T.J., and Fukuba, Y. 2002.
429 Relationship between the curvature constant parameter of the power-duration
430 curve and muscle cross-sectional area of the thigh for cycle ergometry in
431 humans. *Eur. J. Appl. Physiol.* **87**(3): 238-244.
- 432 Souza, K.M., de Lucas, R.D., do Nascimento Salvador, P.C., Guglielmo, L.G.,
433 Caritá, R.A., Greco, C.C., Denadai, B.S. 2015. Maximal power output during
434 incremental cycling test is dependent on the curvature constant of the power-time
435 relationship. *Appl. Physiol. Nutr. Metab.* **40**(9):895-898. doi: 10.1139/apnm-2015-
436 0090.
- 437 Vanhatalo, A., Black, M.I., DiMenna, F.J., Blackwell, J.R., Schmidt, J.F.,
438 Thompson, C., Wylie, L.J., Mohr, M., Bangsbo, J., Krstrup, P., and Jones, A.M.
439 2016. The mechanistic bases of the power-time relationship: muscle metabolic
440 responses and relationships to muscle fibre type. *J. Physiol.* **594**(15): 4407-4423.
441 doi: 10.1113/JP271879.
- 442 Vanhatalo, A., Doust, J.H., and Burnley, M. 2008. A 3-min all-out cycling test is
443 sensitive to a change in critical power. *Med. Sci. Sports Exerc.* **40**(9): 1693-1699.
444 doi: 10.1249/MSS.0b013e318177871a.
- 445 Vanhatalo, A., Doust, J.H., and Burnley, M. 2007. Determination of critical power
446 using a 3-min all-out cycling test. *Med. Sci. Sports Exerc.* **39**(3): 548-555.
- 447 Vanhatalo, A., Fulford, J., DiMenna, F.J., and Jones, A.M. 2010. Influence of
448 hyperoxia on muscle metabolic responses and the power-duration relationship

449 during severe-intensity exercise in humans: a ^{31}P magnetic resonance
450 spectroscopy study. *Exp. Physiol.* **95**(4): 528-540. doi:
451 10.1113/expphysiol.2009.050500.

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452 Table 1. Mean \pm SD values of maximal voluntary contraction (MVC), impulse
453 above end-test torque (IET), and end-test torque (ET) for knee extensors (KE)
454 and plantar flexors (PF) muscle groups. N = 40

	MVC (N·m)	IET (Nm·s)	ET (N·m)
KE	294.9 \pm 62.5	7243.2 \pm 1942.9	84.4 \pm 24.8
PF	181.5 \pm 37.6*	3357.4 \pm 1132.3*	73.9 \pm 19.5*

455 MVC - maximal voluntary contraction; IET - impulse above the end-test torque;
456 ET - end-test torque; KE - knee extensors; PF - plantar flexors. * $p < 0.05$ in
457 relation to KE muscles.

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459 Table 2. Mean \pm SD values of the exercise tolerance (s) obtained during the time
 460 exhaustion tests above (ET + 5%), below (ET - 5%) and at the same percentage
 461 of the maximal voluntary contraction (Similar %MVC) in relation to ET + 5% for
 462 PF. N = 11

	ET + 5%		ET - 5%	Similar %MVC
	Estimated	Actual	Actual	Actual
KE	611.7 \pm 208.1	697.0 \pm 243.7	1030.2 \pm 495.4	156.7 \pm 104.3
PF	255.0 \pm 78.6*	300.7 \pm 156.7*‡	1028.3 \pm 514.4	-

463 KE - knee extensors; PF - plantar flexors. * $p < 0.05$ in relation to KE at the same
 464 exercise condition; ‡ $p < 0.05$ in relation to Similar %MVC condition.

465

466 Figure Captions

467

468 Figure 1. Torque profile during submaximal isometric contraction for a
469 representative subject. Arrow indicates first of three consecutive isometric
470 contraction were the target torque was not attained. Dashed line represents the
471 target torque.

472

473 Figure 2. Mean \pm SD values of torque of knee extensors (KE) and plantar flexors
474 (PF) during the 5-min all-out test. N = 40

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