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1 **The effect of exercise hyperpnea on gross efficiency and anaerobic capacity**
2 **estimates during a 3-min cycle time trial**

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37 **Abstract**

38 This study aimed to analyze the effect of exercise-induced hyperpnea on gross efficiency (GE)
39 and anaerobic capacity estimates during a self-paced 3-min supramaximal cycle time trial (TT).
40 Fourteen highly-trained male cyclists performed 7×4-min submaximal stages, a 6-min passive
41 rest, a 3-min TT, a 5-min passive rest, and a 6-min submaximal stage. Three models were based
42 on the 7×4-min linear regression extrapolation method, using (1) the conventional model (7-
43 Y_{LIN}); (2) the same 7- Y_{LIN} model but correcting for the additional ventilatory cost (i.e.,
44 hyperpnea) (7- $Y_{LIN-V-cor}$); and, (3) accounting for linearly declining GE during the TT (7- Y_{LIN-D}).
45 The other three models were based on GE from the last submaximal stage, using the
46 conventional model (GE_{LAST}) and the same modifications as described for 7+ Y_{LIN} , i.e., (1)
47 GE_{LAST} , (2) $GE_{LAST-V-cor}$, and (3) GE_{LAST-D} . The GE_{LAST} model generated 18% higher values of
48 anaerobic capacity than the 7- Y_{LIN} model ($P<0.05$). During the TT, the hyperpnea corrected
49 model (i.e., 7- $Y_{LIN-V-cor}$ or $GE_{LAST-V-cor}$) generated, compared to the respective conventional
50 model (i.e., 7- Y_{LIN} or GE_{LAST}), ~0.7 percentage points lower GE and ~11% higher anaerobic
51 capacity (all, $P<0.05$). The post-TT GE was 1.9 percentage points lower ($P<0.001$) and the 7-
52 Y_{LIN-D} or GE_{LAST-D} model generated, compared to the respective conventional model, a lower GE
53 (~1.0 percentage points) and ~17% higher anaerobic capacity during the TT (all, $P<0.05$). In
54 conclusion, the correction for a declining GE due to hyperpnea during a supramaximal TT
55 resulted in an increased required total metabolic rate and anaerobic energy expenditure compared
56 to the conventional models.

57

58 **NEW & NOTEWORTHY**

59 This study demonstrates that GE declines during a 3-min supramaximal cycle TT, which is
60 possibly related to the hyperpneic response during supramaximal exercise. The finding from this
61 study also provides novel insight into how the increased ventilatory energy cost from exercise-
62 induced hyperpnea contributes to decreased GE, increased required total metabolic rate, and
63 increased anaerobic energy expenditure during supramaximal exercise. Therefore, conventional
64 linear models for estimating anaerobic capacity are likely to generate underestimated values.

65

66 **Keywords:** endurance exercise, energetics, oxygen deficit, supramaximal exercise, ventilation
67 rate

68

69 INTRODUCTION

70 Two common approaches for estimating the metabolic requirement and anaerobic capacity
71 during supramaximal exercise are the linear regression method, usually referred to as the
72 maximal accumulated oxygen deficit method, and the gross efficiency (GE) method (1, 2). An
73 alternative version of the conventional maximal accumulated oxygen deficit method uses a linear
74 relationship between power output and metabolic rate (i.e., a PO-MR linear-regression method)
75 during submaximal steady-state exercise to estimate the instantaneous required total metabolic
76 rate (i.e., the sum of the aerobic and anaerobic metabolic rates) during supramaximal exercise by
77 extrapolation (3-5). Such a linear relationship can also be used to estimate instantaneous GE
78 during supramaximal exercise, which is of interest when comparing anaerobic capacity estimates
79 generated by different computational models (3, 5). When estimating the required total metabolic
80 rate using the GE method, GE is usually determined during a single submaximal bout at a

81 relatively high exercise intensity ($\sim 70\text{-}80\%$ of maximum oxygen uptake [$\dot{V}O_{2\max}$]), which is used
82 to determine the required total metabolic rate during a subsequent supramaximal effort (2-4). For
83 both the PO-MR linear-regression method and the GE method, the accumulated anaerobic
84 energy expenditure is calculated as the difference between the estimated required total metabolic
85 rate and measured aerobic metabolic rate, integrated over time. For a linear regression between
86 power output and metabolic rate with a positive Y-intercept value, GE increases hyperbolically
87 with increasing power output (6, 7). However, when using the GE method, a fixed value of GE is
88 used, i.e., GE is not assumed to increase with higher power output. Due to these differences, the
89 conventional GE method would likely generate higher values of anaerobic capacity during cycle-
90 ergometry exercise than the linear regression method.

91 Yet both of these methods have been criticized as potentially too simplistic, following
92 observations of a decline in GE after prolonged (~ 60 min at 60% of $\dot{V}O_{2\max}$) submaximal-
93 intensity exercise (8) and/or supramaximal-intensity exercise (9-11). To account for these
94 variations in GE, de Koning et al. (12) suggested a method where GE measured post-exercise
95 could be back-extrapolated to the end of the high-intensity exercise, with the decline in GE from
96 pre-to-post high-intensity exercise being assumed to be proportional with the minute ventilation
97 (i.e., the hyperpneic response). This back-extrapolation of GE has been utilized to estimate
98 anaerobically attributable work in some recent studies (10, 12, 13), with demonstrable
99 differences between the two calculation methods for constant, or declining, GE. Since
100 instantaneous GE can also be calculated during supramaximal exercise by using the linear
101 regression method based on power output and metabolic rate (3, 5), a similar method to the one
102 proposed by de Koning et al. (12) that accounts for a declining GE could potentially also be used
103 in connection with the linear regression method used for determining anaerobic capacity.

104 Yet the back-extrapolation GE method also introduces additional potential confounding factors
105 that may influence the veracity of the estimated GE during supramaximal exercise. For example,
106 excess post-exercise oxygen consumption (EPOC), or recovery oxygen uptake, following a
107 supramaximal exercise task will likely induce some confounding to calculated GE, potentially
108 affecting back-extrapolation and the computed anaerobic contribution to external work (or power
109 output) (14, 15). In addition, non-linear kinetics of carbon dioxide ($\dot{V}CO_2$) elimination by
110 ventilation during and after supramaximal exercise will influence the respiratory exchange ratio
111 (RER), and so may not reflect the actual substrate utilization (11, 16, 17). Therefore,
112 quantification of anaerobic capacity (or anaerobic work capacity) during high-intensity exercise
113 using back-extrapolated GE may prove erroneous due to the influence of the stated confounding
114 factors.

115 An alternative method to account for the potential decline in GE during high-
116 intensity/supramaximal-intensity exercise may be to consider the additional metabolic
117 requirement associated with higher ventilation, i.e., exercise-induced hyperpnea (18). During
118 incremental submaximal exercise up to a ventilation rate of $\sim 105 \text{ L min}^{-1}$ ($\sim 75\%$ of $\dot{V}O_{2\text{max}}$ in
119 endurance-trained males (5)), the oxygen cost of ventilation as a fraction of the oxygen uptake
120 remains relatively constant at $\sim 4\%$ (18). However, due to the exponential rise in the energy cost
121 per liter of ventilation and/or the higher ventilatory equivalent for oxygen, the relative oxygen
122 cost of ventilation may increase to $\sim 15\%$ of $\dot{V}O_{2\text{max}}$ during high-intensity or supramaximal-
123 intensity exercise (18-21). The exponential increase in the oxygen cost of hyperpnea has been
124 proposed to be the main factor for a declining GE during supramaximal exercise (12). Therefore,
125 research where this aspect (i.e., hyperpnea) is integrated into the estimation of GE during high-
126 intensity and/or supramaximal-intensity exercise would be of particular interest to many athletes,

127 coaches, and sports scientists, as this information could be utilized in a variety of different ways
128 (e.g., used for optimizing ventilation patterns, refining pacing strategies, and/or targeting
129 appropriate nutritional needs, etc.). As the oxygen cost of hyperpnea increases exponentially
130 from high-intensity submaximal to supramaximal exercise, failure to integrate this additional
131 oxygen cost during supramaximal exercise would result in an underestimation of the required
132 total metabolic rate, the estimated anaerobic metabolic rate, and the accumulated anaerobic
133 energy expenditure. Yet, to the best of our knowledge, no previous study has considered the
134 effect of the additional metabolic requirement of hyperpnea on GE and anaerobic capacity
135 estimates during supramaximal exercise.

136 Therefore, the current study was designed to analyze, for the first time, the effect of exercise
137 hyperpnea on GE and anaerobic capacity estimates during a self-paced 3-min supramaximal
138 cycle time trial (TT) using the two common methods for calculating anaerobic capacity (i.e., a
139 PO-MR linear regression method [$7-Y_{LIN}$] and a GE method [GE_{LAST}]) with three different
140 variations for each method (i.e., [1] the standard model; [2] with additional ventilation cost
141 during the supramaximal exercise; and [3] accounting for a declining GE), which resulted in a
142 total of six different models. Specifically, the two different calculation methods would be first
143 tested using their default conventional equations (i.e., $7-Y_{LIN}$ and GE_{LAST}); then both corrected
144 for the additional metabolic cost of ventilation (i.e., $7-Y_{LIN-V-COR}$ and $GE_{LAST-V-COR}$); and finally,
145 accounting for a linearly declining GE during the TT ($7-Y_{LIN-D}$; GE_{LAST-D}).

146 The hypotheses of the current study were as follows: 1) the anaerobic capacity estimate would be
147 higher for the GE_{LAST} than the $7-Y_{LIN}$ model, and 2) the anaerobic capacity estimate would be
148 higher for each of the respective hyperpnea-corrected models (i.e., $7-Y_{LIN-V-COR}$ and $GE_{LAST-V-COR}$)
149 compared to the respective conventional model.

150

151 **METHODS**

152 **Participants**

153 Fourteen highly-trained male cyclists (mean \pm SD: age: 26.2 ± 3.7 years, body mass: 74.7 ± 5.9
154 kg, stature: 180.5 ± 6.0 cm) participated in this study (Tier 3–4, McKay et al. (22)). The ethical
155 review board of the University of Salzburg approved the study (EK-GZ: 05/2020). All
156 participants were fully informed about the nature of the study and provided written consent to
157 participate. The participants regularly competed in cycling events and had previously undergone
158 a laboratory performance test on a bike. A criterion for exclusion was a $\dot{V}O_{2\max}$ of $< 55 \text{ ml}\cdot\text{kg}^{-1}$
159 $\cdot\text{min}^{-1}$. On the day of laboratory testing, participants were instructed to have their last regular
160 meal 3-h pre-test and refrain from ingesting caffeine. All participants were familiar with
161 submaximal and maximal cycle ergometry tests.

162

163 **Equipment and testing procedures**

164 The participant's stature and body mass were measured pre-test (Seca 764, Hamburg, Germany).
165 Each participant used their cycling gear (e.g., shoes, cleats, pedals, and clothes) during testing
166 and a Monark LC7TT time-trial bike (Monark Exercise AB, Vansbro, Sweden) was set to the
167 participant's preferences. The LC7TT time-trial bike was equipped with road race handlebars
168 and standard shifting mechanics (Shimano Ultegra 11 Speed, Shimano Inc., Osaka, Japan).
169 Cycling power output was logged continuously as second-by-second data. Respiratory variables
170 were measured using a Cosmed Quark CPET mixing chamber system (Cosmed srl, Rome, Italy)
171 with data as 10-s values. This setup was used to provide valid and reliable metabolic

172 measurements, especially at high ventilation rates in highly trained athletes (23, 24). The gas
173 analyzers were calibrated prior to each test using a known reference gas containing 15.0% O₂
174 and 5% CO₂ (UN 1950 Aerosols, Cortex Biophysik GmbH, Leipzig, Germany) and ambient air.
175 The flowmeter was calibrated with a 3-L syringe (M9424; Medikro Oy, Kuopio, Finland). Blood
176 lactate concentration was determined from an earlobe blood sample (20 μL) and analyzed with a
177 Biosen S-line (EKF diagnostic GmbH, Magdeburg, Germany), which was calibrated with a
178 standard solution of 12 mmol L⁻¹. Heart rate was monitored using a chest strap (Wahoo Kickr,
179 Wahoo Fitness, Atlanta, Georgia, United States) that was connected to the ANT+ receiver of the
180 Cosmed system and synchronously stored with ergospirometry data.

181 A 6-min warm-up was performed at ~37% of peak oxygen uptake ($\dot{V}O_{2\text{peak}}$) and was directly
182 followed by a 7 × 4-min submaximal protocol, at intensities corresponding to ~37-70% (~5.5%
183 increments) of $\dot{V}O_{2\text{peak}}$ and power outputs were determined based on previous test results. After
184 the submaximal protocol, a 6-min passive rest was given to the participant followed by a self-
185 paced 3-min TT that was performed at a maximal effort. Following completion of the TT, the
186 participants passively rested for 5-min, whereafter a 6-min submaximal stage was performed at
187 the same power output as the final submaximal stage prior to the TT. For the warm-up and
188 submaximal stages, the power output was fixed and cadence independent whereas, for the TT,
189 the power output was regulated freely by the athlete via the bike's shifters and was cadence
190 dependent. During all testing, cadence was self-selected by the participant. The cadence for the
191 submaximal exercise was determined as the average of the final minute of each stage.

192 The self-paced 3-min TT was performed with no visible information available regarding
193 physiological response or performance (i.e., heart rate, oxygen uptake, and power output).
194 Participants were instructed to generate the highest possible average power output throughout the

195 TT, with verbal encouragement and information about elapsed time every half minute provided
196 by the test leaders. Blood lactate concentration was measured 5 min into the warm-up, at the end
197 of the 7×4 -min submaximal stages, 1 min before the start of the TT, and 2 min after completion
198 of the TT.

199

200 **Processing of respiratory data**

201 Respiratory and heart rate data were collected continuously during the submaximal exercise and
202 TT. During the submaximal exercise, data from the last minute of each submaximal stage was
203 used for analyzes. To enable a more dynamic respiratory response during the TT, raw respiratory
204 10-s data from the TT were interpolated second-by-second using piecewise constant
205 interpolation for each 10-s average and smoothed using a 9-s counterbalanced moving average
206 (i.e., using a ± 4 -s time window for smoothing), which was conducted twice as described by
207 Lidar et al. (25). The $\dot{V}O_{2\text{peak}}$ and peak ventilation rate were determined as the respective highest
208 20-s moving average during the TT, as based on the raw 10-s respiratory data, while peak heart
209 rate was obtained as the highest 10-s average value. Peak RER was taken over the same period as
210 the $\dot{V}O_{2\text{peak}}$.

211

212 **Calculations**

213 *Submaximal exercise*

214 Energy expenditure was calculated from oxygen uptake ($\dot{V}O_2$) and RER ($\dot{V}CO_2 \cdot \dot{V}O_2^{-1}$) according
215 to the equation introduced by Weir (26) and then converted into a metabolic rate that was based

216 on the average $\dot{V}O_2$, in $L \cdot \text{min}^{-1}$, and RER values (≤ 1.00) during the final minute of each stage of
217 the submaximal exercise protocol.

$$218 \quad MR [W] = \frac{4184(\dot{V}O_2(1.1RER+3.9))}{60} \quad (\text{Eq. 1})$$

219 GE was calculated as:

$$220 \quad GE = \frac{PO [W]}{MR [W]} \quad (\text{Eq. 2})$$

221 Where PO is the power output on the bike.

222 During the submaximal exercise following the TT, the MR was based on the average $\dot{V}O_2$ in
223 $L \cdot \text{min}^{-1}$ during the final minute and using the RER value from the last submaximal stage prior to
224 the TT. This was because RER measured following supramaximal exercise was not considered to
225 reflect the actual substrate utilization due to EPOC and ventilatory dynamics (14, 16, 17). The
226 GE for the submaximal exercise following the TT was calculated as in Eq. 2.

227

228 *The estimation of anaerobic capacity*

229 A linear relationship between PO (W) and metabolic rate (W) during the final minute of each of
230 the 7×4 -min submaximal stages was derived for each participant and referred to as the 7- Y_{LIN}
231 model (Figure 1). The 7- Y_{LIN} regression equation was used to estimate the required
232 instantaneous metabolic rate during the TT ($MR_{\text{TT}_{req}}$) at each 1-s time-point. Submaximal GE
233 based on the last submaximal stage (GE_{LAST}) was also used to estimate the $MR_{\text{TT}_{req}}$ at each 1-s
234 time-point of the TT, with $MR_{\text{TT}_{req}}$ calculated by dividing instantaneous PO with GE_{LAST} . The

235 instantaneous s-by-s GE values during the TT were also calculated for the 7-Y_{LIN} model (GE_{REG})
 236 as instantaneous PO divided by the instantaneous MR calculated from the regression equation.

237 A model was developed to correct for a changing GE during the TT based on the difference in
 238 GE between the last submaximal stage (i.e., GE_{LAST}) and GE measured following the TT
 239 (GE_{TTpost}). To reflect the relative decline in GE at the end-point of the TT (i.e., at 180 s), a ratio
 240 between GE_{TTpost} and GE_{LAST} was used, whereas the GE ratio was set to 1 at the start of the TT.

241 A linear regression was fitted through the GE ratio at the start of the TT (i.e., 1) and the GE ratio
 242 at the end-point of the TT (i.e., GE_{TTpost} divided by GE_{LAST}). The regression equation was used to
 243 determine the GE ratio at each 1-s time-point (*t*) of the TT (GE_{RATIO}). The correction for a
 244 declining (_D) GE during the TT was applied to the original 7-Y_{LIN} and GE_{LAST} models and then
 245 referred to 7-Y_{LIN-D} and GE_{LAST-D}. The MR_{TT_req} at each 1-s time-point (*t*) of the TT was
 246 calculated for 7-Y_{LIN-D} as:

$$247 \quad MR_{TT_req,t}[W] = \frac{PO_{TT,t}[W]}{GE_{REG,t} \times GE_{RATIO,t}} \quad (\text{Eq. 3})$$

248 For GE_{LAST-D}, the MR_{TT_req} at each 1-s time-point (*t*) of the TT was calculated similarly as in Eq.
 249 3, but with the exception that GE_{REG} was changed to GE_{LAST}.

250 For the four models (i.e., 7-Y_{LIN}, GE_{LAST}, 7-Y_{LIN-D}, and GE_{LAST-D}), the instantaneous anaerobic
 251 metabolic rate (MR_{AN}) at each 1-s time-point (*t*) of the TT could then be expressed as:

$$252 \quad MR_{AN,t}[W] = MR_{TT_req,t}[W] - MR_{AE,t}[W] \quad (\text{Eq. 4})$$

253 where MR_{AE} is the aerobic metabolic rate calculated according to Eq. 1 and using an RER of
 254 1.00 (i.e., assuming 100% carbohydrate utilization during the TT).

255 For all four models, the total anaerobic energy expenditure (E_{AN}) was calculated by integrating
256 MR_{AN} over the 3-min TT.

257

258 *The estimation of the metabolic requirement for ventilation*

259 Based on the non-linear relationship for minute ventilation versus respiratory oxygen cost for
260 exercise hyperpnea reported by Dempsey et al. (18), a polynomial third-order equation was
261 constructed but with the oxygen cost of ventilation converted to an energy cost in Joules per liter
262 of ventilation (V_E), assuming 100% carbohydrate utilization and an energy equivalent of 20.92
263 $J \cdot mL[VO_2]^{-1}$. The equation was expressed as:

$$264 \quad VE_{E-COST} [J \cdot L^{-1} V_E] = -1.05217 \times 10^{-5} \times VE^3 + 5.74842 \times 10^{-3} \times VE^2 - 0.520568 \times \\ 265 \quad VE + 48.8437 \quad \text{(Eq. 5)}$$

266 where VE_{E-COST} is the ventilatory energy cost in Joules per liter of V_E .

267 The metabolic requirement for ventilation (MR_{VE} [in W]) was calculated as the product of VE_{E-}
268 $COST$ ($J \cdot L^{-1}$, calculated as in Eq. 5) and respiratory rate ($L \cdot s^{-1}$). The metabolic requirement for
269 ventilation was also expressed as (1) a fraction of the metabolic rate during the submaximal
270 stages; (2) as a fraction of the average aerobic metabolic rate during the TT; and (3) as a fraction
271 of $\dot{V}O_{2peak}$ at the ventilation rate associated with $\dot{V}O_{2peak}$ (calculated by converting $\dot{V}O_{2peak}$ to a
272 peak aerobic metabolic rate [Eq. 1] using an RER of 1.00).

273

274 *The ventilatory corrected models for estimating anaerobic capacity*

275 Eq. 5 was used for estimating the additional metabolic requirement during the TT caused by
276 exercise hyperpnea as described in Figure 2. The increase in VE_{E-COST} with increasing hyperpnea
277 during exercise is shown in Figure 2A. The VE_{E-COST} above that associated with the last
278 submaximal stage was then added to the metabolic requirement estimated during the TT with the
279 $7-Y_{LIN}$ and GE_{LAST} models and were then referred to as the $7-Y_{LIN-V-cor}$ and $GE_{LAST-V-cor}$ models.

280 The additional instantaneous metabolic requirement for ventilation (AMR_{VE}) at each 1-s time-
281 point (t) of the TT was calculated as:

$$282 \quad AMR_{VE,t}[W] = (VE_{E-COST_{TT,t}} - VE_{E-COST_{SUB7}} [J \cdot L^{-1} V_E]) \times TT_{VE,t} [L \cdot s^{-1}] \quad (\text{Eq. 6})$$

283 where $TT_{VE,t}$ is the instantaneous ventilation rate during the TT; $VE_{E-COST_{TT,t}}$ is the
284 instantaneous VE_{E-COST} during the TT; and $VE_{E-COST_{SUB7}}$ is the VE_{E-COST} associated with the
285 last submaximal stage ($SUB7$).

286 $AMR_{VE,t}$ was only calculated for ventilation rates higher than the ventilation rate at the last
287 submaximal stage.

288 The $AMR_{VE,t}$ was added to the $MR_{TT_{req,t}}$ estimated with the $7-Y_{LIN}$ and GE_{LAST} models and
289 thereafter referred to as the $7-Y_{LIN-V-cor}$ and $GE_{LAST-V-cor}$ models (i.e., the ventilatory corrected
290 [V-cor] models).

291 The instantaneous anaerobic metabolic rate for the $7-Y_{LIN-V-cor}$ and $GE_{LAST-V-cor}$ models was
292 calculated as in Eq. 4 and the E_{AN} was calculated by integrating MR_{AN} over the 3-min TT.

293

294 *The estimation of GE and anaerobic work capacity during supramaximal exercise*

295 The instantaneous GE at each 1-s time-point (t) of the TT ($GE_{TT,t}$) was calculated as:

296
$$GE_{TT,t} = \frac{PO_{TT,t}[W]}{MR_{TT,t}[W]} \quad (\text{Eq. 7})$$

297 where $MR_{TT,t}$ is the model-specific instantaneous required metabolic rate. This calculation was
 298 performed for the 7-Y_{LIN}, 7-Y_{LIN-V-cor}, GE_{LAST-V-cor}, 7-Y_{LIN-D}, and GE_{LAST-D} models. The
 299 calculation was redundant for the GE_{LAST} model as that assumes a constant GE (i.e., the same
 300 GE as for the last submaximal stage).

301 Anaerobic PO contribution (PO_{AN_cont}) (i.e., PO attributable to MR_{AN}) at each 1-s time-point (t)
 302 of the TT was calculated for the 7-Y_{LIN}, GE_{LAST}, 7-Y_{LIN-V-cor}, GE_{LAST-V-cor}, 7-Y_{LIN-D}, and GE_{LAST-}
 303 _D models as:

304
$$PO_{AN_{cont},t}[W] = PO_{TT,t}[W] - (MR_{AE,t}[W] \times GE_{TT,t}) \quad (\text{Eq. 8})$$

305 where $PO_{TT,t}$ is the PO during the TT and $MR_{AE,t}$ is the aerobic metabolic rate.

306 The anaerobic work capacity in Joules was calculated for the six models by integrating the
 307 model-specific PO_{AN_cont} (W) over the TT duration (s).

308

309 *The estimated relative effect of hyperpnea on the change in GE between pre- and post-TT*
 310 *measures*

311 To calculate a GE value for the post-TT submaximal bout that was independent of a changing
 312 MR_{VE} ($GE_{IND_{MR_{VE}}}$), the following equation was used:

313
$$GE_{IND_{MR_{VE}}} = \frac{PO_{SUB}[W]}{MR_{SUB_post} - (MR_{VE_{post}} - MR_{VE_{pre}})[W]} \quad (\text{Eq. 9})$$

314 Where PO_{SUB} is the submaximal power output (was the same for pre-and post-TT measures of
 315 GE), MR_{SUB_post} is the post-TT submaximal metabolic rate (in W), MR_{VE_post} is the post-TT

316 metabolic requirement for ventilation (in W), and MR_{VE_pre} is the pre-TT metabolic requirement
317 for ventilation (in W).

318 The percentage point difference in GE between SUB7 and GE_{TTpost} was compared with the
319 percentage point difference in GE between SUB7 and $GE_IND_{MR_VE}$. Based on these data the
320 relative effect of exercise hyperpnea on the change in GE from pre-to-post TT submaximal
321 exercise could be evaluated.

322

323 **Statistics**

324 Data were checked for normality by visual inspection of Q-Q plots and histograms together with
325 the Shapiro-Wilks analysis and are presented as mean \pm standard deviation (SD), except in the
326 case of RPE and peak heart rate where data are presented as median and interquartile range
327 (IQR). The linear relationship between power output and metabolic rate was assessed using
328 linear regression analysis. A one-way repeated measures ANOVA test was used to compare GE
329 between the seven submaximal stages. The six different model-specific estimated values of GE,
330 required metabolic rate, anaerobic capacity, and anaerobic work capacity associated with the TT
331 were also compared with one-way repeated measures ANOVA tests. In addition, the
332 methodological error was evaluated via the overall standard error of measurement (SEM)
333 calculated as the square root of the within-subjects mean square error term in the repeated-
334 measures ANOVA. For the ANOVA tests, the assumption of sphericity was tested using
335 Mauchly's test and for violated sphericity, Greenhouse-Geisser correction of the degrees of
336 freedom was used (epsilon was ≤ 0.75). Eta squared effect size (η^2) was also reported for the
337 ANOVA tests. Bonferroni α corrections were applied to all ANOVA tests. A paired *t*-test was

338 used to compare physiological responses, GE, and perceived effort associated with submaximal
339 exercise during the seventh submaximal stage prior to the TT versus the same submaximal
340 exercise after the TT. The mean difference \pm 95% limits of agreement for the respective pair-
341 wise comparisons of the six anaerobic capacity estimates were evaluated by using Bland-Altman
342 calculations (27). The pair-wise mean difference was also tested with a paired-sample *t*-test. In
343 addition, the absolute typical error for the comparisons was computed, which was also expressed
344 as a percentage (i.e., relative to the grand mean). For the paired *t*-tests, the standardized mean
345 difference (Hedges' g_{av} , effect size [$ES_{Hg_{av}}$]) was computed according to the equations presented
346 by Lakens (28). All statistical tests were processed using Office Excel 2016 (Microsoft
347 Corporation, Redmond, WA, USA) and the Statistical Package for the Social Sciences (SPSS 25,
348 IBM Corp., Armonk, NY, USA). The level of statistical significance was set at $\alpha \leq 0.05$.

349

350 **RESULTS**

351 The submaximal power outputs, cadences, physiological responses, and GE associated with the
352 seven submaximal stages (SUB₁₋₇) of cycle ergometry exercise, and the post time trial
353 submaximal bout are shown in Table 1. The GE was shown to be power output dependent as
354 revealed by the significant differences between the seven submaximal stages ($F_{2,28} = 18.8$, $P <$
355 0.001 , $\eta^2 = 0.591$) with significant pairwise differences being indicated in Table 1. The blood
356 lactate concentrations 1 min prior to the first submaximal stage (after a 5-min warm-up) and
357 immediately after the seventh submaximal stage were 0.9 ± 0.1 and 2.2 ± 0.8 mmol·L⁻¹,
358 respectively. The average metabolic rates for the 7-Y_{LIN} model are displayed in Figure 1A and
359 GE values are presented in Figure 1B.

360 The 3-min TT was completed at an average power output of 399 ± 42 W at an average cadence
361 of 93 ± 11 rev \cdot min⁻¹. The average $\dot{V}O_2$ was 50 ± 4 ml \cdot kg⁻¹ \cdot min⁻¹ (3.8 ± 0.5 L \cdot min⁻¹) and the
362 $\dot{V}O_{2peak}$ was 66 ± 6 ml \cdot kg⁻¹ \cdot min⁻¹ (4.9 ± 0.6 L \cdot min⁻¹, 1.71 ± 0.22 kW) at an RER of 1.11 ± 0.08 .
363 The peak ventilation rate and peak heart rate were 183 ± 26 L \cdot min⁻¹ and 181 (IQR = 179-183)
364 beats \cdot min⁻¹, respectively. The blood lactate concentrations 1 min pre and 2 min post the TT were
365 1.9 ± 0.5 and 10.9 ± 2.0 mmol \cdot L⁻¹, respectively. The median RPE measured immediately after
366 the TT was 19 (IQR = 19-20). Respiratory responses and the estimated ventilatory energy cost
367 per liter of ventilation as well as the estimated metabolic rate required for ventilation during the
368 TT are shown in Table 1. The ventilation rate at $\dot{V}O_{2peak}$ was 181 ± 27 L \cdot min⁻¹, which resulted in
369 an estimated ventilatory energy cost of 81 ± 14 J \cdot L $[V_E]$ ⁻¹ and an estimated metabolic rate
370 required for ventilation of 250 ± 80 W, which was equivalent to $14.4 \pm 3.4\%$ of $\dot{V}O_{2peak}$.

371 The difference in physiological responses between the last submaximal stage prior to the TT, and
372 the submaximal stage following the TT, are shown in Table 1. For the same power output ($3.30 \pm$
373 0.30 W \cdot kg⁻¹), the physiological responses were higher for all variables except for RER, whereas
374 GE was 1.9 percentage points lower than prior to the TT. Approximately one-third (29%) of the
375 1.9 percentage point decline in GE could be related to the higher ventilatory energy expenditure
376 due to the 27% higher ventilation rate and the 20% higher ventilatory energy cost per liter of
377 ventilation.

378 Figure 2A shows the relationship between ventilation rate (L \cdot min⁻¹) and ventilatory energy cost
379 (J \cdot L $[V_E]$ ⁻¹) adapted from Dempsey et al. (1996). Figure 2B shows the average instantaneous
380 ventilation rate during the TT and Figure 2C shows the additional instantaneous metabolic
381 requirement for respiration that was added to the required metabolic rate estimated with the 7-
382 Y_{LIN} and GE_{LAST} models, and thereafter referred to as the 7- $Y_{LIN-V-cor}$ and $GE_{LAST-V-cor}$ models.

383 Figure 3 shows the average effect on the required total metabolic rate, GE, and anaerobic
384 metabolic rate when the estimated additional metabolic rate due to hyperpnea was added to the
385 $7\text{-}Y_{\text{LIN}}$ and GE_{LAST} models, i.e., the results for the two ventilation corrected models ($7\text{-}Y_{\text{LIN-V-cor}}$
386 and $\text{GE}_{\text{LAST-V-cor}}$).

387 When comparing the $7\text{-}Y_{\text{LIN}}$ versus the GE_{LAST} model, the $7\text{-}Y_{\text{LIN}}$ model resulted in a 0.9
388 percentage point higher GE associated with the TT, a 5% lower required total metabolic rate, a
389 15% lower anaerobic capacity, and an 11% lower anaerobic work capacity (see Table 2). The
390 correction for an increased metabolic requirement due to hyperpnea (i.e., the $7\text{-}Y_{\text{LIN-V-cor}}$ and
391 $\text{GE}_{\text{LAST-V-cor}}$ models) resulted in ~ 0.7 percentage points lower GE, $\sim 3\%$ higher required total
392 metabolic rate, $\sim 11\%$ higher anaerobic capacity, and $\sim 9\%$ higher anaerobic work capacity for the
393 $7\text{-}Y_{\text{LIN-V-cor}}$ and $\text{GE}_{\text{LAST-V-cor}}$ models combined versus the GE_{LAST} and $7\text{-}Y_{\text{LIN}}$ models combined.
394 The mean differences, limits of agreement, and typical errors for the pair-wise comparisons of
395 the six various models are presented in Figure 4.

396

397 **DISCUSSION**

398 This study has systematically analyzed the effect of exercise hyperpnea on GE and anaerobic
399 capacity estimates during a self-paced 3-min supramaximal cycle TT. For the two conventional
400 models that were compared, the GE_{LAST} model generated higher values of anaerobic capacity
401 than the $7\text{-}Y_{\text{LIN}}$ model, due to the positive Y-intercept value for the $7\text{-}Y_{\text{LIN}}$ model, which
402 assumes an increasing GE with higher power outputs for the $7\text{-}Y_{\text{LIN}}$ model. When correcting for
403 hyperpnea during the TT (i.e., $7\text{-}Y_{\text{LIN-V-cor}}$ and $\text{GE}_{\text{LAST-V-cor}}$), GE values were ~ 0.7 percentage
404 points lower than for the conventional models (i.e., $7\text{-}Y_{\text{LIN}}$ and GE_{LAST}), which resulted in

405 significantly higher values of the required metabolic rate (~3.2%) and anaerobic capacity (~11%)
406 during the TT. The GE measured after the TT was 1.9 percentage points lower than prior to the
407 TT.

408 The significantly higher values of anaerobic capacity (18%) observed with the GE_{LAST} than 7-
409 Y_{LIN} model confirmed the study hypothesis. This finding was explained by the positive Y-
410 intercept in the 7- Y_{LIN} regression (Figure 1A) and the increasing GE with higher power output
411 (Figure 1B), which is contrary to the GE_{LAST} model that assumes a constant GE. On average, this
412 resulted in a 0.9 percentage point higher GE during the TT for the 7- Y_{LIN} than the GE_{LAST} model.
413 This finding differs from the results of previous studies that utilized different exercise modalities,
414 such as diagonal-stride roller-skiing or running on a treadmill, where a linear regression model
415 (power output/speed versus metabolic rate) without a baseline (i.e., “resting”) value of metabolic
416 rate generated similar values of anaerobic capacity as a model based on a fixed value of GE
417 and/or gross energy cost (4, 5, 29). This was due to the close-to-zero average Y-intercept value
418 for the respective linear regression model in these previous studies.

419 A novel aspect of the current study was the inclusion of an estimated additional metabolic cost of
420 ventilation for exercise intensities that were above the exercise intensity of the last submaximal
421 stage; as demonstrated in Figure 2. Thus, the additional instantaneous metabolic rate due to
422 hyperpnea during the TT was calculated and added to the total metabolic requirement generated
423 by the 7- Y_{LIN} and GE_{LAST} models (Figure 2C) with the average effect presented in Figure 3. Due
424 to the ventilatory response during the TT (see Figures 2B-C), the instantaneous GE started to
425 decline after approximately the first minute of exercise and continued to gradually decline
426 throughout the TT (see Figures 3C-D). This resulted in a higher anaerobic metabolic rate for
427 each respective ventilatory-corrected model, compared to each respective conventional model,

428 during the last two minutes of exercise (Figures 3E-F). When correcting for hyperpnea during
429 the TT, the GE was, on average, ~ 0.7 percentage points lower compared to the conventional
430 model (i.e., $7 \cdot Y_{\text{LIN}}$ or GE_{LAST}), and anaerobic capacity values were $\sim 11\%$ higher (or $0.14 \text{ kJ} \cdot \text{kg}^{-1}$
431 higher). As shown in Figures 4E and 4H, the higher anaerobic capacity estimates due to
432 hyperpnea ranged between $0.05\text{-}0.27 \text{ kJ} \cdot \text{kg}^{-1}$, indicating considerable inter-participant variation.
433 This is not a surprising result as the magnitude of additional ventilatory energy cost is related to
434 the absolute ventilation rate during exercise (Figure 2A), which has also been considered in
435 previous studies (18, 21).

436 To account for a declining GE during supramaximal cycle exercise, de Koning et al. (12)
437 suggested an alternative back-extrapolation approach compared to the conventional GE method.
438 However, this back-extrapolated approach has some methodological issues and requires several
439 problematic assumptions. For example, oxygen uptake recovery (also known as EPOC) after a
440 high-intensity/supramaximal-intensity effort is curvilinear due to the respective fast and slow
441 components (14, 15). Also, the nonlinear $\dot{V}\text{CO}_2$ kinetics after maximal exercise is likely to
442 generate a post-exercise RER that does not reflect actual substrate utilization (11, 14, 17). For
443 example, in the current study, the RER measured during the submaximal bout after the TT was
444 0.80 , which was substantially lower than the RER of 0.90 that was measured prior to the TT (see
445 Table 1). However, it is highly unlikely that substrate utilization shifts towards a higher relative
446 fat utilization after a supramaximal TT, indicating that the measured RER did not accurately
447 reflect the true substrate utilization. Due to these aforementioned problems, GE in the current
448 study was measured during the final minute of a 6-min submaximal stage that started 5 min after
449 the TT. Since the RER measured during the submaximal exercise following the TT was not
450 considered to reflect substrate utilization, the RER value from the same steady-state submaximal

451 exercise prior to the TT (i.e., the seventh submaximal stage) was used in the calculation of
452 metabolic rate and GE. It should be acknowledged that the revised models of the present study
453 are based on theoretical constructs, and are thus unlikely to calculate the exact quantity of
454 anaerobic capacity, due to the complex physiological systems. However, this caveat is also
455 pertinent to the original models and should be considered an inherent flaw in all anaerobic
456 capacity calculations.

457 Similar to previous research (10-13), GE was found to be lower during the submaximal exercise
458 that followed the supramaximal TT than before. Interestingly, a considerable part of this 1.9-
459 percentage-point lower GE could be related to the increased metabolic requirement for
460 ventilation due to the $\sim 25 \text{ L}\cdot\text{min}^{-1}$ higher ventilation rate and the estimated $\sim 20\%$ higher energy
461 cost per liter of ventilation. Other potential factors to the lower GE after the supramaximal TT
462 could have been attributed to impaired muscle contractility and/or altered muscle recruitment
463 patterns (11, 30). One major factor for the higher ventilation rate during the submaximal exercise
464 bout that followed the TT, than prior to the TT, was likely mainly related to an increased
465 ventilatory drive, i.e., lower ventilatory recruitment threshold of the ventilatory response, caused
466 by lower blood pH (acidosis) due to anaerobic glycolysis from the prior 3-min supramaximal TT
467 (16). Both the $7\text{-}Y_{\text{LIN-D}}$ and $7\text{-}Y_{\text{LIN-V-cor}}$ models generated higher values of anaerobic capacity
468 than the conventional $7\text{-}Y_{\text{LIN}}$ model (Figures 4D, E), a result that also was similar to the GE
469 method-based models (Figures 4G, H). One clear difference between the $7\text{-}Y_{\text{LIN}}$ and GE_{LAST}
470 models is presented in Figure 1, where the $7\text{-}Y_{\text{LIN}}$ model assumes a slightly increasing GE with
471 higher power outputs, whereas the GE_{LAST} model assumes a constant GE during the TT based on
472 the GE value from the seventh submaximal stage. Due to the decline in GE during supramaximal
473 exercise, the $7\text{-}Y_{\text{LIN}}$ likely underestimated anaerobic capacity. In contrast, the GE_{LAST} model may

474 have provided a more valid estimate due to the lower GE value used for calculating the required
475 metabolic rate (see Figures 3C-D). The corrections made for a declining GE during the TT in
476 connection with the $7\text{-}Y_{\text{LIN}}$ model, i.e., the $7\text{-}Y_{\text{LIN-V-cor}}$ and $7\text{-}Y_{\text{LIN-D}}$ models, probably generated
477 more valid estimates of anaerobic capacity compared to the conventional $7\text{-}Y_{\text{LIN}}$ model. On the
478 other hand, the corrections made for a declining GE during the TT in connection with the GE_{LAST}
479 model, i.e., the $\text{GE}_{\text{LAST-V-cor}}$ and $\text{GE}_{\text{LAST-D}}$, may have overestimated the anaerobic capacity.

480 From these observations, we conclude that GE declines during a 3-min supramaximal cycle TT.
481 A major cause of this decline is likely related to the concave-upward relationship of ventilation
482 rate versus ventilatory energy cost (see Figure 2A) and the ventilatory response during
483 supramaximal exercise with a higher ventilatory equivalent for oxygen. Therefore, conventional
484 linear regression models that do not account for a declining GE during supramaximal cycle-
485 ergometry exercise may underestimate the total metabolic requirement and, thus, the
486 accumulated anaerobic energy expenditure. In the current study, the relationship between
487 ventilation rate and ventilatory energy cost was adapted from data presented by Dempsey et al.
488 (18) and was assumed to remain consistent across participants, i.e., no inter-participant variation.
489 We recognize that this assumption was a simplification of the probable individual variation, as a
490 high individual variation in this relationship has been previously observed (21). Based on the
491 results presented in Table 1 and Figure 2A, a very minor part of the increased requirement for
492 ventilation was likely already included in the $7\text{-}Y_{\text{LIN}}$ model. This is because the estimated relative
493 metabolic rate required for ventilation increased from 4.5% at the first submaximal stage to 5.4%
494 at the last submaximal stage (see Table 1). Nevertheless, this part is likely to be very marginal as
495 the ventilatory equivalent for oxygen increased substantially during the TT and so did also the
496 ventilatory energy cost per liter of ventilation (see Table 1). Due to these issues, a more refined

497 methodology would include a separate test to establish the individual polynomial relationships
498 between ventilation rate and ventilatory oxygen cost (or estimated energy cost) (18, 19, 21). For
499 example, a participant could mimic different exercise ventilation rates during rest, i.e., different
500 levels of enforced hyperventilation at rest using a CO₂-enriched gas mixture to avoid the
501 participant from fainting (21). Such an analysis would also allow for a more holistic
502 understanding of the importance of respiratory energy/oxygen cost on exercise performance. For
503 instance, the method provided in this study would make it possible to estimate the individual
504 effect of hyperpnea on GE (or gross energy cost), which is an important performance factor in
505 many sports (31). In addition, different ventilation strategies/patterns, pacing strategies, and/or
506 altitudes may potentially induce different hyperpneic responses that could result in altered
507 metabolic requirements for ventilation which in turn could influence GE and exercise
508 performance. Further studies could potentially determine the specific effect(s) of respiratory
509 training and/or respiratory muscle fatigue on high-intensity endurance performances (32, 33).
510 Other areas of interest could be to analyze the potential effect of exercise-induced hyperpnea,
511 and/or respiratory muscle fatigue (18, 34, 35), on the $\dot{V}O_2$ slow component during high-intensity
512 submaximal exercise (11, 35, 36).

513

514 **CONCLUSIONS**

515 The current study shows that for the two conventional models that were compared, the GE_{LAST}
516 model generated higher values of anaerobic capacity than the 7-Y_{LIN} model, an effect caused by
517 the different GE assumptions during supramaximal exercise. The two hyperpnea corrected
518 models (i.e., 7-Y_{LIN-V-cor} and GE_{LAST-V-cor}) generated, on average, a 0.7 percentage point lower
519 GE estimate during the TT, which resulted in an 11% higher anaerobic capacity estimate

520 compared to the respective conventional models. In addition, a substantial part of the decline in
521 GE after the TT was estimated to be caused by the higher ventilation rate, and, thus, the
522 increased metabolic requirement for ventilation, that followed the supramaximal exercise.
523 Therefore, these findings suggest that the conventional linear model (i.e., $7 \cdot Y_{LIN}$) for estimating
524 anaerobic capacity is likely to generate underestimated values.

525

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530

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535

536 **DISCLOSURES**

537 No conflicts of interest, financial or otherwise, are declared by the authors.

538

539 **AUTHOR CONTRIBUTIONS**

540 E.A. designed the study whereas P.B. and T.S. were responsible for the data collection. E.A.
541 analyzed and interpreted the data. E.A. and J.O. wrote the first draft of the article. All listed
542 authors drafted the manuscript, revised the manuscript and approve the final version to be
543 published and agree to be accountable for all aspects of the work.

544

545 REFERENCES

546 1. **Medbø JI, Mohn AC, Tabata I, Bahr R, Vaage O, and Sejersted OM.** Anaerobic
547 capacity determined by maximal accumulated O₂ deficit. *J Appl Physiol* 64: 50-60, 1988.
548 doi:10.1152/jappl.1988.64.1.50.

549 2. **Noordhof DA, Vink AM, de Koning JJ, and Foster C.** Anaerobic capacity: effect of
550 computational method. *Int J Sports Med* 32: 422-428, 2011. doi:10.1055/s-0031-1271676.

551 3. **Andersson EP, Bachl P, Schmuttermair A, Staunton CA, and Stöggl TL.** Anaerobic
552 work capacity in cycling: the effect of computational method. *Eur J Appl Physiol* 2022.
553 doi:10.1007/s00421-022-05038-7.

554 4. **Andersson EP, and McGawley K.** A comparison between different methods of
555 estimating anaerobic energy production. *Front Physiol* 9: 82, 2018.
556 doi:10.3389/fphys.2018.00082.

557 5. **Andersson EP, Noordhof DA, and Lögdal N.** The anaerobic capacity of cross-country
558 skiers: the effect of computational method and skiing sub-technique. *Front Sports Act Living* 2:
559 2020. doi:10.3389/fspor.2020.00037.

560 6. **Ettema G, and Lorås HW.** Efficiency in cycling: a review. *Eur J Appl Physiol* 106: 1-
561 14, 2009. doi:10.1007/s00421-009-1008-7.

- 562 7. **MacDougall KB, Falconer TM, and MacIntosh BR.** Efficiency of cycling exercise:
563 Quantification, mechanisms, and misunderstandings. *Scand J Med Sci Sports* 32: 951-970, 2022.
564 doi:10.1111/sms.14149.
- 565 8. **Passfield L, and Doust JH.** Changes in cycling efficiency and performance after
566 endurance exercise. *Med Sci Sports Exerc* 32: 1935-1941, 2000. doi:10.1097/00005768-
567 200011000-00018.
- 568 9. **Beneke R, Pollmann C, Bleif I, Leithauser RM, and Hutler M.** How anaerobic is the
569 Wingate Anaerobic Test for humans? *Eur J Appl Physiol* 87: 388-392, 2002.
570 doi:10.1007/s00421-002-0622-4.
- 571 10. **Noordhof DA, Mulder RC, Malterer KR, Foster C, and de Koning JJ.** The decline in
572 gross efficiency in relation to cycling time-trial length. *Int J Sports Physiol Perform* 10: 64-70,
573 2015. doi:10.1123/ijsp.2014-0034.
- 574 11. **Sahlin K, Sorensen JB, Gladden LB, Rossiter HB, and Pedersen PK.** Prior heavy
575 exercise eliminates VO₂ slow component and reduces efficiency during submaximal exercise in
576 humans. *J Physiol* 564: 765-773, 2005. doi:10.1113/jphysiol.2005.083840.
- 577 12. **de Koning JJ, Noordhof DA, Uitslag TP, Galiart RE, Dodge C, and Foster C.** An
578 approach to estimating gross efficiency during high-intensity exercise. *Int J Sports Physiol*
579 *Perform* 8: 682-684, 2013. doi:10.1123/ijsp.8.6.682.
- 580 13. **Mulder RC, Noordhof DA, Malterer KR, Foster C, and de Koning JJ.** Anaerobic
581 work calculated in cycling time trials of different length. *Int J Sports Physiol Perform* 10: 153-
582 159, 2015. doi:10.1123/ijsp.2014-0035.

- 583 14. **Børsheim E, and Bahr R.** Effect of exercise intensity, duration and mode on post-
584 exercise oxygen consumption. *Sports Med* 33: 1037-1060, 2003. doi:10.2165/00007256-
585 200333140-00002.
- 586 15. **Piiper J, and Spiller P.** Repayment of O₂ debt and resynthesis of high-energy
587 phosphates in gastrocnemius muscle of the dog. *J Appl Physiol* 28: 657-662, 1970.
588 doi:10.1152/jappl.1970.28.5.657.
- 589 16. **Duffin J.** Role of acid-base balance in the chemoreflex control of breathing. *J Appl*
590 *Physiol* 99: 2255-2265, 2005. doi:10.1152/jappphysiol.00640.2005.
- 591 17. **Ward SA, Whipp BJ, Koyal S, and Wasserman K.** Influence of body CO₂ stores on
592 ventilatory dynamics during exercise. *J Appl Physiol Respir Environ Exerc Physiol* 55: 742-749,
593 1983. doi:10.1152/jappl.1983.55.3.742.
- 594 18. **Dempsey JA, Harms CA, and Ainsworth DM.** Respiratory muscle perfusion and
595 energetics during exercise. *Med Sci Sports Exerc* 28: 1123-1128, 1996. doi:10.1097/00005768-
596 199609000-00007.
- 597 19. **Aaron EA, Johnson BD, Seow CK, and Dempsey JA.** Oxygen cost of exercise
598 hyperpnea: measurement. *J Appl Physiol* 72: 1810-1817, 1992.
599 doi:10.1152/jappl.1992.72.5.1810.
- 600 20. **Aaron EA, Seow KC, Johnson BD, and Dempsey JA.** Oxygen cost of exercise
601 hyperpnea: implications for performance. *J Appl Physiol* 72: 1818-1825, 1992.
602 doi:10.1152/jappl.1992.72.5.1818.
- 603 21. **Vella CA, Marks D, and Robergs RA.** Oxygen cost of ventilation during incremental
604 exercise to VO₂ max. *Respirology* 11: 175-181, 2006. doi:10.1111/j.1440-1843.2006.00825.x.

- 605 22. **McKay AKA, Stellingwerff T, Smith ES, Martin DT, Mujika I, Goosey-Tolfrey VL,**
606 **Sheppard J, and Burke LM.** Defining training and performance caliber: a participant
607 classification framework. *Int J Sports Physiol Perform* 17: 317-331, 2022.
608 doi:10.1123/ijsp.2021-0451.
- 609 23. **Nieman DC, Austin MD, Dew D, and Utter AC.** Validity of COSMED's quark CPET
610 mixing chamber system in evaluating energy metabolism during aerobic exercise in healthy male
611 adults. *Res Sports Med* 21: 136-145, 2013. doi:10.1080/15438627.2012.757227.
- 612 24. **Winkert K, Kirsten J, Dreyhaupt J, Steinacker JM, and Treff G.** The COSMED K5
613 in breath-by-breath and mixing chamber mode at low to high intensities. *Med Sci Sports Exerc*
614 52: 1153-1162, 2020. doi:10.1249/mss.0000000000002241.
- 615 25. **Lidar J, Andersson EP, and Sundström D.** Validity and reliability of hydraulic-
616 analogy bioenergetic models in sprint roller skiing. *Front Physiol* 12: 2021.
617 doi:10.3389/fphys.2021.726414.
- 618 26. **Weir JB.** New methods for calculating metabolic rate with special reference to protein
619 metabolism. *J Physiol* 109: 1-9, 1949. doi:10.1113/jphysiol.1949.sp004363.
- 620 27. **Bland JM, and Altman DG.** Measuring agreement in method comparison studies. *Stat*
621 *Methods Med Res* 8: 135-160, 1999. doi:10.1177/096228029900800204.
- 622 28. **Lakens D.** Calculating and reporting effect sizes to facilitate cumulative science: a
623 practical primer for t-tests and ANOVAs. *Front Psychol* 4: 863, 2013.
624 doi:10.3389/fpsyg.2013.00863.
- 625 29. **Andersson EP, Björklund G, and McGawley K.** Anaerobic capacity in running: the
626 effect of computational method. *Front Physiol* 12: 2021. doi:10.3389/fphys.2021.708172.

- 627 30. **Poole DC, Schaffartzik W, Knight DR, Derion T, Kennedy B, Guy HJ, Prediletto R,**
628 **and Wagner PD.** Contribution of exercising legs to the slow component of oxygen uptake
629 kinetics in humans. *J Appl Physiol* 71: 1245-1260, 1991. doi:10.1152/jappl.1991.71.4.1245.
- 630 31. **Joyner MJ, and Coyle EF.** Endurance exercise performance: the physiology of
631 champions. *J Physiol* 586: 35-44, 2008. doi:10.1113/jphysiol.2007.143834.
- 632 32. **Illi SK, Held U, Frank I, and Spengler CM.** Effect of respiratory muscle training on
633 exercise performance in healthy individuals: a systematic review and meta-analysis. *Sports Med*
634 42: 707-724, 2012. doi:10.1007/bf03262290.
- 635 33. **Romer LM, and Polkey MI.** Exercise-induced respiratory muscle fatigue: implications
636 for performance. *J Appl Physiol* 104: 879-888, 2008. doi:10.1152/japplphysiol.01157.2007.
- 637 34. **Dempsey JA.** New perspectives concerning feedback influences on cardiorespiratory
638 control during rhythmic exercise and on exercise performance. *J Physiol* 590: 4129-4144, 2012.
639 doi:10.1113/jphysiol.2012.233908.
- 640 35. **O'Connell JM, Weir JM, and MacIntosh BR.** Blood lactate accumulation decreases
641 during the slow component of oxygen uptake without a decrease in muscular efficiency. *Pflugers*
642 *Arch* 469: 1257-1265, 2017. doi:10.1007/s00424-017-1986-y.
- 643 36. **Jones AM, Grassi B, Christensen PM, Krstrup P, Bangsbo J, and Poole DC.** Slow
644 component of VO₂ kinetics: mechanistic bases and practical applications. *Med Sci Sports Exerc*
645 43: 2046-2062, 2011. doi:10.1249/MSS.0b013e31821fcfc1.

646

647 **FIGURE CAPTIONS**

648 **Figure 1.** (A) The average metabolic rates associated with the seven stages of submaximal
649 exercise (Sub stages 1-7) and the extrapolated average total metabolic rate for the supramaximal

650 self-paced 3-min time trial (TT_{AVG}). The black line represents the linear regression line ($7-Y_{LIN}$)
651 based on the average data with the dotted lines representing the \pm SD for the linear regression
652 line. (B) The gross efficiencies for the seven stages of submaximal exercise (yellow tilted
653 squares) and the average gross efficiency for the TT_{AVG} as calculated from the regression
654 equation in A (i.e., power output divided by the total metabolic rate during the TT). The black
655 line (in B) represents the gross efficiency relationship calculated from the linear regression
656 equation presented in A with the dotted lines representing the \pm SD.

657

658 **Figure 2.** (A) The effect of an increased ventilation rate on the energy cost of ventilation (VE_{E-}
659 $COST$). The relationship was adapted from Dempsey et al. (16) with further details provided in the
660 methods. The dashed green vertical lines indicate the average ventilation range for the seven
661 submaximal stages in the current study. The dashed red horizontal line is based on the average
662 ventilation rate associated with the last submaximal stage and represents the average boundary
663 for additional metabolic requirement due to exercise hyperpnea during the supramaximal time-
664 trial (TT) effort (i.e., the TT average cut off). (B) The average instantaneous second-by-second
665 ventilatory response during the 3-min supramaximal TT. (C) The average additional
666 instantaneous metabolic rate due to hyperpnea during the TT, calculated as VE_{E-COST} above the
667 last submaximal stage multiplied by the ventilation rate in liters per second (see the methods for
668 further details). The estimated additional instantaneous MR due to hyperpnea during the TT was
669 added to the total metabolic requirement generated by the $7-Y_{LIN}$ and GE_{LAST} models and then
670 referred to as the $7-Y_{LIN-V-cor}$ and $GE_{LAST-V-cor}$ models (i.e., the ventilatory corrected [V-cor]
671 models).

672

673 **Figure 3.** The power output and the estimated required total metabolic rates (MR_{REQ}) for (A)
674 GE_{LAST} and $GE_{LAST-V-cor}$, and (B) $7-Y_{LIN}$ and $7-Y_{LIN-V-cor}$ models during the 3-min self-paced
675 cycle time trial (TT). The $7-Y_{LIN}$ is the linear model based on seven submaximal stages and the
676 GE_{LAST} is the model based on the GE value from the last submaximal stage. The $7-Y_{LIN-V-cor}$ and
677 $GE_{LAST-V-cor}$ are the same models but with the estimated additional metabolic rate due to
678 hyperpnea added to the $7-Y_{LIN}$ and GE_{LAST} models. (C-D) The instantaneous second-by-second
679 gross efficiency values for the different models during the TT. (E-F) The instantaneous second-
680 by-second aerobic metabolic rate (MR_{AE}) and the estimated anaerobic metabolic rate (MR_{AN}) as
681 based on the different models during the TT. The presented data are based on group-average
682 values.

683

684 **Figure 4.** Bland-Altman plots for the six various models of estimating anaerobic capacity (AnC)
685 associated with the 3-min self-paced cycle time trial. Bland-Altman plots represent the mean
686 difference ($MEAN_{DIFF}$) in the $AnC \pm 95\%$ (1.96 SD) limits of agreement between the methods.
687 Abbreviations: AnC_{DIFF} , the difference in AnC; TE, typical error (in parenthesis: typical error
688 expressed as a percentage of the grand mean); ES, Hedges's g_{av} effect size (Hg_{av}), $7-Y_{LIN}$, the $7 \times$
689 4-min linear regression model; GE_{LAST} , the gross efficiency model based on the last submaximal
690 stage; $7-Y_{LIN-V-cor}$, the exercise hyperpnea corrected $7-Y_{LIN}$ model; $GE_{LAST-V-cor}$, the exercise
691 hyperpnea corrected GE_{LAST} model; $7-Y_{LIN-D}$, the $7-Y_{LIN}$ model corrected for a declining GE;
692 GE_{LAST-D} , the GE_{LAST} model corrected for a declining GE.

Table 1. Mean \pm SD values of power outputs, physiological responses, and gross efficiencies associated with the seven submaximal stages (SUB₁-SUB₇), the 3-min supramaximal time trial (TT), and the post-time-trial submaximal stage (SUB_{TTpost}) of cycle ergometry exercise.

	SUB ₁	SUB ₂	SUB ₃	SUB ₄	SUB ₅	SUB ₆	SUB ₇	TT	SUB _{TTpost}	ES
Power output (W·kg ⁻¹)	1.54 \pm 0.14	1.84 \pm 0.16	2.13 \pm 0.19	2.42 \pm 0.22	2.72 \pm 0.24	3.01 \pm 0.27	3.30 \pm 0.30	5.34 \pm 0.43	3.30 \pm 0.30	-
Cadence (rev·min ⁻¹)	69 \pm 5	71 \pm 5	74 \pm 5	77 \pm 5	80 \pm 5	83 \pm 5	86 \pm 5	93 \pm 11	87 \pm 7	0.3
Heart rate (% of TT _{peak})	60 \pm 6	64 \pm 6	67 \pm 6	72 \pm 6	77 \pm 5	82 \pm 5	86 \pm 5	-	91 \pm 4 ^S	0.9
MR _{AE} (W·kg ⁻¹)	8.3 \pm 1.2	9.4 \pm 1.3	10.6 \pm 1.3	11.8 \pm 1.6	13.1 \pm 1.6	14.4 \pm 1.6	15.8 \pm 1.7	17.7 \pm 1.4	17.4 \pm 1.7 ^S	0.9
MR _{AE} (% of MR _{AE_peak})	36 \pm 6	42 \pm 7	47 \pm 7	52 \pm 8	58 \pm 9	64 \pm 9	69 \pm 9	-	76 \pm 9 ^S	0.7
\dot{V}_E (L·min ⁻¹)	45.6 \pm 8.2	50.9 \pm 9.7	57.3 \pm 10.3	64.3 \pm 10.3	72.5 \pm 11.2	81.0 \pm 12.9	90.7 \pm 15.6	130.5 \pm 23.1	115.6 \pm 20.6 ^S	1.3
VE _{E-COST} (J·L[V _E] ⁻¹)	36 \pm 1	36 \pm 1	36 \pm 1	37 \pm 1	38 \pm 2	39 \pm 3	42 \pm 4	61 \pm 9	50 \pm 8 ^S	1.2
MR _{VE} (W·kg ⁻¹)	0.4 \pm 0.1	0.4 \pm 0.1	0.5 \pm 0.1	0.5 \pm 0.1	0.6 \pm 0.1	0.7 \pm 0.1	0.9 \pm 0.2	2.0 \pm 0.6	1.3 \pm 0.4 ^S	1.4
MR _{VE_rel} (% of MR _{AE})	4.5 \pm 0.3	4.3 \pm 0.3	4.4 \pm 0.3	4.5 \pm 0.3	4.7 \pm 0.4	4.9 \pm 0.5	5.4 \pm 0.9	10.2 \pm 2.4	7.5 \pm 1.9 ^S	1.3
$\dot{V}_E \cdot \dot{V}O_2^{-1}$	24.6 \pm 1.7	24.0 \pm 1.7	24.1 \pm 1.5	24.5 \pm 1.6	24.8 \pm 1.3	25.2 \pm 1.5	26.0 \pm 2.2	34.8 \pm 3.5	30.3 \pm 3.2 ^S	1.5
$\dot{V}_E \cdot \dot{V}CO_2^{-1}$	28.6 \pm 2.1	28.1 \pm 2.3	28.0 \pm 2.2	28.1 \pm 2.5	28.3 \pm 2.3	28.4 \pm 2.3	28.9 \pm 2.9	33.5 \pm 3.1	37.5 \pm 4.4 ^S	2.2
RER ($\dot{V}CO_2 \cdot \dot{V}O_2^{-1}$)	0.86 \pm 0.04	0.86 \pm 0.04	0.86 \pm 0.05	0.87 \pm 0.04	0.88 \pm 0.05	0.89 \pm 0.05	0.90 \pm 0.05	1.03 \pm 0.09	0.80 \pm 0.04 ^S	-2.1

Gross efficiency (%)	18.8 ± 2.0 ^{c-g}	19.7 ± 2.1 ^d	20.2 ± 1.8	20.7 ± 1.8	20.8 ± 1.4	20.9 ± 1.3	21.0 ± 1.3	-	19.1 ± 1.2 ^s	-1.4
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Abbreviations: ES, effect size; TT_{peak}, TT peak value; MR_{AE}, aerobic metabolic rate; MR_{AE_peak}, peak aerobic metabolic rate from the TT; \dot{V}_E , ventilation rate; VE_{E-COST}, ventilatory energy cost; V_E, ventilation volume; MR_{VE}, the estimated metabolic rate required for ventilation (i.e., VE_{E-COST} [J·L⁻¹] × \dot{V}_E [L·s⁻¹]); MR_{VE_rel}, the estimated metabolic rate required for ventilation expressed as a fraction of the MR_{AE}; $\dot{V}_E \cdot \dot{V}O_2^{-1}$, ventilatory equivalent for oxygen; $\dot{V}_E \cdot \dot{V}CO_2^{-1}$, ventilatory equivalent for carbon dioxide; RER, respiratory exchange ratio. Statistical comparisons were performed between SUB_{TTpost} and SUB₇. ^s*P* < 0.001 versus SUB₇. Hedges' *g*_{av} ES (*Hg*_{av}) was presented for the respective pair-wise comparisons. A one-way repeated measures ANOVA was used to compare the gross efficiency values for the seven submaximal stages. ^{c-g}Significantly different from SUB₃, SUB₄, SUB₅, SUB₆, and SUB₇, all *P* < 0.01. ^dSignificantly different from SUB₄, *P* = 0.01.

Table 2. Mean \pm SD values of the gross efficiency, metabolic requirement, anaerobic capacity, anaerobic work capacity, and relative anaerobic energy contribution during the 3-min cycle time trial (TT) for the six different calculation models.

	Model of calculation						F-value	P-value	η^2	SEM
	7-Y _{LIN}	7-Y _{LIN-V-cor}	7-Y _{LIN-D}	GE _{LAST}	GE _{LAST-V-cor}	GE _{LAST-D}				
GE _{TT_avg} (%)	21.9 \pm 1.4 ^{b,f}	21.2 \pm 1.3 ^{e,f}	20.9 \pm 1.3 ^f	21.0 \pm 1.3 ^{e,f}	20.4 \pm 1.3	20.0 \pm 1.2	F _{2,21} = 23.4	< 0.001	0.643	0.89
MR _{TT_req} (W·kg ⁻¹)	24.3 \pm 1.9 ^{b,f}	25.1 \pm 2.0 ^{e,f}	25.4 \pm 2.2 ^f	25.5 \pm 2.4 ^{e,f}	26.3 \pm 2.6	26.6 \pm 2.7	F _{5,65} = 21.8	< 0.001	0.627	0.66
MR _{TT_req} (% of MR _{ae_peak})	106 \pm 4 ^{b,f}	110 \pm 4 ^{e,f}	111 \pm 5 ^f	111 \pm 6 ^{e,f}	115 \pm 6	116 \pm 6	F _{5,65} = 24.1	< 0.001	0.650	2.72
AnC (kJ·kg ⁻¹)	1.19 \pm 0.27 ^{b,f}	1.33 \pm 0.25 ^{e,f}	1.41 \pm 0.32 ^f	1.40 \pm 0.31 ^{e,f}	1.54 \pm 0.31	1.63 \pm 0.36	F _{5,65} = 23.6	< 0.001	0.645	0.12
AnWC (kJ·kg ⁻¹)	0.26 \pm 0.05 ^{b,f}	0.29 \pm 0.05 ^{e,f}	0.30 \pm 0.06 ^f	0.29 \pm 0.06 ^{e,f}	0.32 \pm 0.05	0.33 \pm 0.06	F _{2,22} = 25.0	< 0.001	0.658	0.03
AN _{rel} (% of total)	27 \pm 5 ^{b,f}	29 \pm 4 ^{e,f}	31 \pm 5 ^f	30 \pm 5 ^{e,f}	32 \pm 4 ^f	34 \pm 5	F _{2,20} = 27.6	< 0.001	0.680	3.01

Abbreviations: 7-Y_{LIN}, the 7 \times 4-min linear regression model; GE_{LAST}, the gross efficiency model based on the last submaximal stage; 7-Y_{LIN-V-cor}, the exercise hyperpnea corrected 7-Y_{LIN} model; GE_{LAST-V-cor}, the exercise hyperpnea corrected GE_{LAST} model; 7-Y_{LIN-D}, the 7-Y_{LIN} model corrected for a declining GE; GE_{LAST-D}, the GE_{LAST} model corrected for a declining GE; SEM, standard error of measurement; GE_{TT_avg}, average GE during the TT; MR_{TT_req}, required total metabolic rate during the TT; MR_{ae_peak}, peak aerobic metabolic rate during the TT; AnC, anaerobic capacity; AnWC, anaerobic work capacity; AN_{rel}, relative anaerobic energy contribution. F-values, P-values, and eta squared effect size (η^2) were obtained by a one-way ANOVA. ^bStatistically significantly different from 7-

$Y_{\text{LIN-V-cor}}$ ($P < 0.05$). ^cStatistically significantly different from $7\text{-}Y_{\text{LIN-D}}$ ($P < 0.05$). ^dStatistically significantly different from GE_{LAST} ($P < 0.05$). ^eStatistically significantly different from $\text{GE}_{\text{LAST-V-cor}}$ ($P < 0.05$). ^fStatistically significantly different from $\text{GE}_{\text{LAST-D}}$ ($P < 0.05$).

The effect of exercise hyperpnea on gross efficiency and anaerobic capacity estimates during a 3-min cycle time trial

METHODS



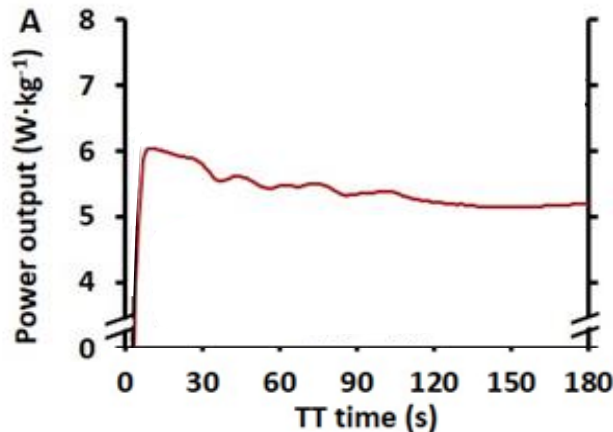
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Highly-trained cyclists

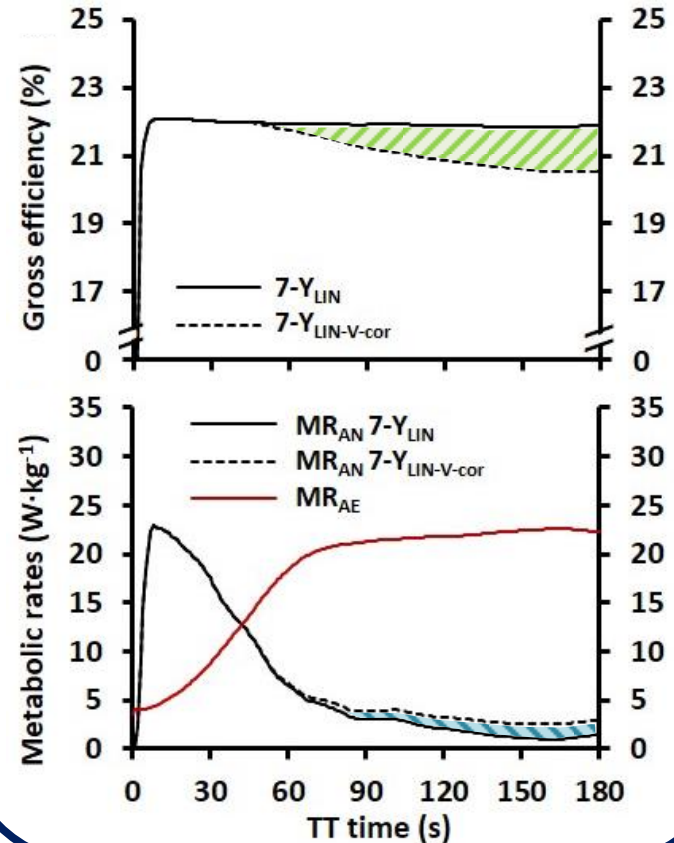


3-min

Time trial



OUTCOME



CONCLUSION

Exercise-induced hyperpnea decreased gross efficiency and increased required total metabolic rate and anaerobic energy expenditure during supramaximal exercise. Estimation models should include the additional energy cost from increased ventilatory energy requirements.

