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1           **Physiological Comparison between Non-Athletes, Endurance, Power and Team Athletes**

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15           8       **Running head:** (an)aerobic power in athletes

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24 **Abstract**

25 We hypothesized that endurance athletes have lower muscle power than power athletes due to a  
26 combination of weaker and slower muscles, while their higher endurance is attributable to better oxygen  
27 extraction, reflecting a higher muscle oxidative capacity and larger stroke volume.

28 Endurance ( $n=87$ ; distance runners, road cyclists, paddlers, skiers), power ( $n=77$ ; sprinters, throwers,  
29 combat sport athletes, body builders), team ( $n=64$ ; basketball, soccer, volleyball) and non-athletes  
30 ( $n=223$ ) performed a countermovement jump and an incremental running test to estimate their maximal  
31 anaerobic and aerobic power ( $VO_{2max}$ ), respectively. Dynamometry and M-mode echocardiography  
32 were used to measure muscle strength and stroke volume. The  $VO_{2max}$  ( $L \cdot min^{-1}$ ) was larger in  
33 endurance and team athletes than in power athletes and non-athletes ( $p<0.05$ ). Athletes had a larger  
34 stroke volume, left ventricular mass and left ventricular wall thickness than non-athletes ( $p<0.02$ ), but  
35 there were no significant differences between athlete groups. The higher anaerobic power in power and  
36 team athletes than in endurance athletes and non-athletes ( $p<0.001$ ) was associated with a larger force  
37 ( $p<0.001$ ), but not faster contractile properties. Endurance athletes (20.6%) had a higher ( $p<0.05$ )  
38 aerobic:anaerobic power ratio than controls and power and team athletes (14.0-15.3%). The larger  
39 oxygen pulse, without significant differences in stroke volume, in endurance than power athletes  
40 indicates a larger oxygen extraction during exercise. Power athletes had stronger, but not faster, muscles  
41 than endurance athletes. The similar  $VO_{2max}$  in endurance and team athletes and similar jump power  
42 in team and power athletes, suggests that concurrent training does not necessarily impair power or  
43 endurance performance.

45 **Keywords:** maximal oxygen uptake, jumping power, anaerobic capacity, performance

46 **Abbreviations:**  $BF_{max}$  maximal breathing frequency; BM, body mass; BMI, body mass index; CV,  
47 coefficient of variation; EF, ejection fraction;  $FEV_1$ , forced expiratory volume in one second; FVC,  
48 forced vital capacity; Hb, haemoglobin; HR, heart rate; LV, left ventricle; LVM, left ventricular mass;  
49 MVC, maximal voluntary contraction torque; PEF, predicted peak expiratory flow; RWT, relative left  
50 cardiac ventricle wall thickness; RWT, relative left ventricular wall thickness; SV, stroke volume;  
51  $VE_{max}$ , maximal pulmonary ventilation;  $VO_{2max}$ , maximal oxygen uptake;  $VT_{max}$ , tidal volume.

52

## 53 Introduction

54 The human body has a remarkable ability to respond to altered functional demands. Exercise training  
55 programs exploit this plasticity, where in general at the one end endurance is gained by regular exercise  
56 of a moderate intensity and long duration, and at the other end power is gained by regular high-intensity  
57 short-duration exercise (Saltin and Gollnick 1983). In team sports, both power and endurance are  
58 required. For instance, a football game lasts for a significant time, requiring endurance, and is  
59 characterized by short sprints, breaks and quick turns that require high power.

60 Power is the product of force and velocity and it is unclear whether the lower power in endurance than  
61 power athletes (Grassi et al. 1991; Michaelis et al. 2008), defined here as athletes not specializing in  
62 endurance events, is attributable solely to a lower force generating capacity and/or slower contractile  
63 properties of muscles from endurance athletes. Indeed, fast fibers not only contract faster, but can also  
64 produce more than three times the power of slow fibers (Gilliver et al. 2009). Yet, some studies have  
65 shown a decrease (Erskine et al. 2011; Hather et al. 1991) rather than an increase in the proportion of  
66 the fast type IIx/IIb fibers in response to resistance training, which would, if that were the only change,  
67 result in a lower rather than a higher power in power athletes. The velocity of a contraction is, however,  
68 not only related to the fiber type composition, but also decreases with increasing load according to the  
69 force-velocity relationship (Degens 2019). In other words, if the velocity at which peak power is  
70 developed for a given 'body mass to maximal isometric force ratio' is lower in endurance than in power  
71 athletes it indicates a reduced velocity. Applying this concept to ageing muscles, we have shown that  
72 part of the reduction in muscle power in old age is attributable to slower contractile properties (Maden-  
73 Wilkinson et al. 2015). It thus remains to be determined to what extent the higher jumping power in  
74 power than endurance athletes is related to their faster contractile properties and/or a larger force  
75 generating capacity of the muscle.

76 The alleged trade-off, or Principle of Allocation, between endurance and power performance in athletes  
77 (Degens 2012; van Wessel et al. 2010; Boullosa et al. 2013) suggests that endurance athletes are  
78 unlikely to be very successful in power events and *vice versa*. However, such negative correlations  
79 between power and endurance performance are rather poor in decathletes (Van Damme et al. 2002),

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80 implying that many athletes perform well in both endurance and power events in the decathlon. Further  
81 support for the notion that power and endurance can go together comes from athletes that excel in both  
82 sprinting and long distance running (Eynon et al. 2011). Finally, the maximal oxygen uptake (VO<sub>2</sub>max)  
83 of endurance athletes is not negatively affected by additional resistance exercise, and endurance  
84 performance may even improve (Hickson et al. 1988; Vikmoen et al. 2016; Boullosa et al. 2013). In  
85 fact, resistance and power training can also increase stroke volume and VO<sub>2</sub>max (Kraemer et al. 1988;  
86 Venckunas et al. 2011). Furthermore, we previously observed that there were no significant differences  
87 in the ventilatory function of master power and endurance athletes (Degens et al. 2013). While  
88 endurance and resistance training are considered to elicit different physiological adaptations, these  
89 observations suggest that there is no strict dichotomy between power and endurance athletes.

90 The aim of the present study was to characterize the physiological adaptations in power, endurance and  
91 team athletes. We hypothesized that endurance athletes have lower muscle power than power and team  
92 athletes due to both slower and weaker muscles, while their higher endurance is attributable to a larger  
93 stroke volume, lower body mass and higher oxidative capacity of the muscle. Based on the alleged  
94 trade-off, or Principle of Allocation, between endurance and power performance we expected that  
95 superimposing regular resistance training to an endurance program or *vice versa* will reduce  
96 performance in power events at the expense of endurance and *vice versa*.

97

## 98 **Methods**

### 99 *Study design*

100 The participants were 17-37-year-old men, aka GELAK cohort (Genetics and Epigenetics of Lithuanian  
101 Athletes from Kaunas). They were excluded from participation if they were diagnosed with  
102 cardiovascular diseases or hypertension. Athletes were recreational to elite level and were recruited  
103 from the Registers of the Lithuanian Sports Federations during the competitive period as described  
104 previously (Karaliute et al. 2011; Malinauskas et al. 2014). According to self-reporting, they had been  
105 training 3-14 times a week (Malinauskas et al. 2014). The study was approved by the Lithuanian

106 National Committee for Bioethics, and adhered to the guidelines of the declaration of Helsinki and the  
107 ethical standards described in (Harriss and Atkinson 2015). Participants provided written informed  
108 consent before participating. Athletes were divided into 3 groups: endurance athletes ( $n=87$ ; distance  
109 runners,  $n=50$ ; orienteers,  $n=11$ ; road cyclists,  $n=10$ ; triathletes,  $n=5$ ; walkers,  $n=4$ ; skiers,  $n=3$ ; modern  
110 pentathletes,  $n=2$ , a paddler and a rally participant), power/strength athletes ( $n=77$ ; strength athletes,  
111  $n=17$ ; track and field sprinters,  $n=16$ , combat sport athletes,  $n=18$ ; aerobics,  $n=6$ ; boxers,  $n=5$ ; body  
112 builders,  $n=4$ ; fitness athletes,  $n=3$  throwers,  $n=3$ ; divers,  $n=2$ ; sprint swimmers,  $n=2$  and a deacathlete)  
113 and team athletes ( $n=64$ ; basketball,  $n=49$ ; soccer,  $n=11$ , volleyball,  $n=2$ , and a badminton and a  
114 handball player). Non-athletes ( $n=223$ ) trained for less than 2 h per week for the last 5 years. The body  
115 mass index was calculated as body mass divided by height squared (BMI in  $\text{kg}\cdot\text{m}^{-2}$ ). We measured  
116 subscapular, triceps, biceps, chest, lower arm, hand, abdominal, supra-iliac, thigh and lower leg skinfold  
117 thickness and presented the sum of skinfolds. Table 1 shows the participant characteristics.

118

#### 119 *Shuttle run test*

120 As a measure of anaerobic performance and agility, the participants performed a 10x5 m shuttle-run  
121 test (Venckunas et al. 2017; Christou et al. 2006) on a concrete floor. The test consisted of five  
122 consecutive 10-m laps that had to be completed as fast as possible. An experienced investigator  
123 measured the time with a hand-held stopwatch. The participants were familiarized with the test by one  
124 or two submaximal laps followed by 2 min rest.

125

#### 126 *Countermovement jump*

127 As a measure of maximal leg muscle power (Maden-Wilkinson et al. 2015; Bagley et al. 2019), the  
128 participants performed three countermovement jumps (hands on the waist and no swing) on a contact  
129 mat (Newtest Powertimer Testing System, Oulu, Finland), each separated by at least 1 min to prevent  
130 fatigue. The best jump was used for further analysis. Jump velocity at take-off ( $v$  in  $\text{m}\cdot\text{s}^{-1}$ ) was calculated  
131 as:

132 
$$v = a * t_f/2$$

133 where ‘a’ is the gravitational acceleration (9.81 m·s<sup>-2</sup>) and ‘t<sub>f</sub>’ the flight time of the jump. The flight  
134 time was the time from take-off (no force recorded on the platform) until landing (the moment that  
135 forces on the platform are registered again). The power (in Watts) of the countermovement jump was  
136 given as an estimate of Maximal Anaerobic Power and calculated as:

137 
$$W = \text{body mass} * a * v$$

138  
139 *Maximal voluntary contraction*

140 Before assessment of the maximal knee extension torque the participants performed a few submaximal  
141 extensions/flexions to familiarize with the procedures. Maximal knee extension torque (MVC) in each  
142 leg was measured during three consecutive, without rest interval, maximal effort full-range isokinetic  
143 flexion–extension contraction cycles at 30°·s<sup>-1</sup> on a dynamometer (Biodex Pro3, USA). The maximum  
144 extension torque of three consecutive attempts for each leg was determined and the average of the two  
145 legs was used for further analysis.

146  
147 *Maximal incremental exercise test*

148 To measure VO<sub>2</sub>max, a ramp treadmill (H/P/Cosmos Sports & Medical GMBH, Germany) protocol of  
149 continuous incremental running speed until exhaustion was applied. The participants started the test by  
150 jogging at 7 km·h<sup>-1</sup> for 3 min at an initial gradient of 1%, and then the speed of the treadmill belt  
151 increased by 0.1 km·h<sup>-1</sup> every 6 seconds. When the treadmill speed reached 20 km·h<sup>-1</sup> the speed was  
152 not increased further, but the gradient of the treadmill was increased by 0.05% every 6 s. Throughout  
153 the test, breath-by-breath gas analysis was performed using an Oxycon Mobile gas analyzer (Viasys,  
154 Germany), and heart rate (HR) was recorded with a HR meter 810s (Polar, Finland). VO<sub>2</sub>max was  
155 considered to be reached when the heart rate reached >90% predicted maximal heart rate, the respiratory  
156 exchange ratio (RER) was > 1.1 and the participant could not continue running at the required pace



157 despite encouragement.  $VO_{2max}$ , maximal heart rate, maximal breathing frequency ( $BF_{max}$ ), tidal  
158 volume ( $VT_{max}$ ) and maximal ventilation ( $VE_{max}$ ) during the test were calculated from averaged 20-  
159 second intervals and maximal aerobic power calculated (Wasserman et al. 2005). Participants received  
160 verbal encouragement throughout the test.

161

#### 162 *Aerobic:anaerobic power ratio*

163 The ratio of the maximal power generated during the  $VO_{2max}$  test to the power during jumping was  
164 presented as the aerobic:anaerobic power ratio (Bagley et al. 2019). A higher ratio reflects that at  
165  $VO_{2max}$  a larger proportion of total available power is generated.

166

#### 167 *Spirometry*

168 It has been suggested that pulmonary function may limit exercise performance in elite endurance  
169 athletes (McKenzie 2012) and indeed a positive relationship has been found between  $VO_{2max}$  and  
170 arterial partial oxygen pressure at  $VO_{2max}$  (Nielsen 2003). Therefore, lung function was determined  
171 with standard spirometry as described previously (Degens et al. 2013). The percentage predicted values  
172 were obtained by using equations for the use of a facemask (Wohlgemuth et al. 2003).

173

#### 174 *Cardiac parameters*

175 Stroke volume (SV), ejection fraction (%EF), left ventricular mass and relative left ventricular wall  
176 thickness (RWT) were determined at rest as described previously (Karaliute et al. 2011; Venckunas et  
177 al. 2008) in the M-mode with a 2-4 MHz probe connected to a Sonosite Titan ultrasound scanner  
178 (Sonosite, Bothell, WA, USA). The oxygen pulse was calculated as the  $VO_{2max}$  divided by maximal  
179 heart rate. Oxygen extraction from the blood was estimated as (assuming the increase in SV during  
180 exercise is similar in all groups): the oxygen pulse divided by  $1.75 \times$  resting SV (assuming an

181 approximately 75% increase in SV during exercise (Zhou et al. 2001)), giving the  $VO_2$  per SV (mL  
1  
2 182  $O_2 \cdot mL^{-1}$ ) during maximal exercise.  
3

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5 183 Since hemoglobin is the main carrier of oxygen, a finger-prick blood sample was taken to determine  
6  
7 184 the hemoglobin concentration in a ClinCheckAlpha (Biochemical Systems International, Arezzo, Italy).  
8  
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10 185

### 11 12 13 186 *Statistics*

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15  
16 187 The reproducibility of several measures over a year was determined in 20 participants as the coefficient  
17  
18 188 of variation (CV). The CV was calculated as follows:

$$19 189 \quad \quad \quad CV=100 \cdot SD_{dif} / \mu$$

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24 190 where  $SD_{dif}$  represents the standard deviation of the difference between repeated measurements and  $\mu$   
25  
26 191 represents the mean of the pooled test-retest data.

27  
28  
29 192 ANOVA with a Bonferroni-corrected post-hoc test was used to assess differences between groups. The  
30  
31 193 Shapiro-Wilk test showed that the data were normally distributed. Pearson correlation coefficients  
32  
33 194 represented relationships between parameters. Differences were considered significant at  $p < 0.05$ .  
34  
35 195 Descriptive data is shown as mean  $\pm$  SD.  
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### 40 41 42 197 **Results**

43  
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45 198 The CVs were: maximal heart rate 2.5%, left ventricular mass 17.6%, SV 9.5%, %EF 8.4%,  $VE_{max}$   
46  
47 199 9.1%,  $VT_{max}$  11.2%,  $BF_{max}$  12.6%,  $VO_{2max}$  8.8%.  
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49

50 200 Non-athletes were on average 2 years older than athletes ( $p < 0.001$ ; Table 1). The body mass and BMI  
51  
52 201 were lowest in endurance athletes ( $p < 0.05$ ) and higher in power athletes than in non-athletes ( $p < 0.001$ ).  
53

54 202 While team athletes were taller than participants in all other groups ( $p < 0.001$ ), their body mass and  
55  
56 203 BMI did not differ significantly from non-athletes. The sum of the skinfold thicknesses was smaller in  
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204 the athletes than non-athletes ( $p < 0.001$ ) and higher in power than endurance athletes ( $p < 0.001$ ) (Table  
1). Athletes performed the shuttle run in a shorter time than non-athletes ( $p \leq 0.016$ ; Table 1).

206 The  $\text{VO}_2\text{max}$  in  $\text{L} \cdot \text{min}^{-1}$  of athletes was higher than that of non-athletes ( $p \leq 0.002$ ), where endurance  
207 and team athletes had a higher  $\text{VO}_2\text{max}$  than power athletes ( $p \leq 0.014$ ; Fig 1A).  $\text{VO}_2\text{max}$  normalized to  
208 body mass was higher in endurance athletes than in any other group ( $p < 0.001$ ), but the difference  
209 between power athletes and non-athletes had disappeared (Fig. 1B).

210 The maximal heart rate and hemoglobin concentration did not differ significantly between groups.  
211 Athletes had a larger stroke volume ( $p \leq 0.009$ ) and left ventricular mass ( $p < 0.001$ ) than non-athletes  
212 (Table 1). The RWT was larger in endurance and power athletes than non-athletes ( $p < 0.001$ ), but there  
213 was no significant difference between team athletes and non-athletes (Table 1). Endurance athletes had  
214 a larger stroke volume per body mass than any other group ( $p \leq 0.003$ ; Fig. 1C). Endurance and team  
215 athletes had a larger oxygen pulse than power athletes and non-athletes ( $p \leq 0.001$ ; Fig. 1D). The oxygen  
216 pulse per stroke volume was larger in endurance athletes than in non-athletes and power athletes  
217 ( $p \leq 0.015$ ; Table 1).

218 The  $\text{VE}_{\text{max}}$  per body mass was higher in endurance athletes than in any other group ( $p < 0.001$ ; Table 1).  
219 This was realized by both a higher  $\text{VT}_{\text{max}}$  per body mass ( $\text{mL} \cdot \text{kg}^{-1}$ ) in endurance than in power and team  
220 athletes ( $p \leq 0.02$ ), and higher  $\text{BF}_{\text{max}}$  ( $p < 0.001$ ) than in non-athletes and power athletes (Table 1). This  
221 was, however, not related to a better ventilatory function in endurance athletes than in the other groups,  
222 as team athletes, for instance, had a better  $\text{FEV}_{1\text{pred}}$  than endurance athletes ( $p < 0.05$ ; Table 1).

223 Non-athletes achieved the least ( $p < 0.001$ ) and endurance athletes the highest ( $p \leq 0.034$ ) maximal power  
224 during the progressive  $\text{VO}_2\text{max}$  test (Table 1).

225 Jumping power was lowest in endurance athletes and highest in power and team athletes, with that of  
226 non-athletes in between ( $p < 0.001$ ; Fig. 2A). Normalized to body mass, the difference between  
227 endurance athletes on the one hand and power and team athletes on the other disappeared, but non-  
228 athletes developed less power than power and team athletes ( $p < 0.001$ ; Table 1). Endurance athletes and  
229 non-athletes had a lower maximal  $30^\circ \cdot \text{s}^{-1}$  knee extension torque than the power and team athletes

230 (p<0.001; Fig. 2B). The velocity at take-off was higher in power and team athletes than non-athletes  
231 and endurance athletes (p<0.001; Fig. 2C).

232 VO<sub>2</sub>max (mL·min<sup>-1</sup>) correlated positively with stroke volume (R<sup>2</sup>=0.16; p<0.001). The velocity at take-  
233 off correlated inversely with the body mass:maximal 30 °·s<sup>-1</sup> knee extension torque ratio (R<sup>2</sup>=0.226;  
234 p<0.001; Figure 2D) and this ratio was lower in athletes than non-athletes (p≤0.008) and lower in team  
235 than endurance athletes (p=0.032; Table 1).

236 The ratio of aerobic to peak power during the jump was higher in endurance athletes than in any of the  
237 other groups (p<0.0005) and was higher in team athletes than in non-athletes (p≤0.008; Table 1).

238 There were no significant relationships between the performance in the shuttle run test with VO<sub>2</sub>max,  
239 maximal 30°·s<sup>-1</sup> knee extension torque or maximal jumping power per body mass (data not shown).

240

## 241 Discussion

242 The main observation of the present study is that the larger anaerobic (jumping) power of power and  
243 team athletes than endurance and non-athletes is largely attributable to their larger muscle strength, and  
244 not to faster muscle contractile properties. The power at VO<sub>2</sub>max is only about 21% of anaerobic power  
245 in endurance athletes and just 15% in non-athletes and power athletes. The higher oxygen pulse in  
246 endurance and team athletes than power athletes, and similar hemoglobin concentrations and stroke  
247 volumes, left ventricular mass and wall thickness, suggest that the endurance and team athletes realized  
248 part of their larger VO<sub>2</sub>max via enhanced oxygen extraction. The observation that team athletes had a  
249 similar VO<sub>2</sub>max to endurance athletes and a similar jump power as power athletes suggests that at least  
250 in our population superimposing regular resistance training to an endurance program or *vice versa* will  
251 not reduce performance in power events at the expense of endurance and *vice versa*

252

253 *Shuttle run test*

254 The shuttle run test is considered to test leg power and agility. Our data suggest that this may not be the  
255 case as both power and endurance athletes were faster than non-athletes, where only the power athletes  
256 had a larger jumping power per body mass. We also found no relationship between the performance in  
257 the shuttle run test and countermovement jump. A similar pattern was seen in pubertal boys who showed  
258 an improved shuttle run performance after both soccer and soccer + strength training, while the  
259 countermovement jump performance was improved only in the soccer + strength training group  
260 (Christou et al. 2006). The shuttle run test may thus be more an indicator of agility than power.

261

### 262 *Aerobic power*

263 In all athletic groups the  $VO_2\text{max}$  in  $L \cdot \text{min}^{-1}$  was higher than in non-athletes, with power athletes having  
264 a lower  $VO_2\text{max}$  than team and endurance athletes, something also seen previously (Bassett and Howley  
265 2000; Bagley et al. 2019). The larger stroke volume in athletes than non-athletes undoubtedly  
266 contributes to their higher  $VO_2\text{max}$ , but this does not explain the difference in  $VO_2\text{max}$  between athlete  
267 groups as they all had a similar stroke volumes, at least at rest. These observations challenge the idea  
268 that resting stroke volume differs between endurance and power training (Fagard 2003) and with the  
269 similar left ventricular mass and wall thickness indicate that cardiac adaptations are similar in endurance  
270 and power athletes. The larger  $VO_2\text{max}$  in endurance than power athletes has therefore to be explained  
271 by other factors than differences in structural cardiac adaptations, such as a larger oxygen carrying  
272 capacity and/or oxygen extraction by endurance athletes. All groups had a similar [Hb] indicating a  
273 similar oxygen carrying capacity of the blood. The stroke volume at rest did not differ significantly  
274 between power and endurance athletes. If we assume that the stroke volume increases similarly during  
275 exercise, as seen in trained and untrained people, except for elite endurance athletes (Zhou et al. 2001),  
276 it suggests that the oxygen extraction from the blood was higher in endurance and team than in power  
277 athletes. Indeed, it has been suggested that the  $VO_2\text{max}$  during whole body exercise is primarily  
278 determined by the oxygen transport capacity and to a lesser extent by peripheral factors (capillary  
279 transfer and mitochondrial volume), even after endurance training, but the significance of the peripheral  
280 factors may increase with endurance training (di Prampero and Ferretti 1990). Indeed, an increased

1  
2 282 oxygen extraction may be realized by a higher capillary density in endurance athletes, that increases the  
3  
4 283 gas-exchange area in the muscle, and an increased mitochondrial network, that increases the oxygen  
5  
6 284 gradient, and hence the oxygen flux, from the capillary to the mitochondria (Saltin and Gollnick 1983;  
7  
8 di Prampero and Ferretti 1990).

9  
10 285 Although spirometry did not differ much between athletes and non-athletes, as we have seen before in  
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12 286 master athletes (Degens et al. 2013), the maximal exercise-induced ventilation was higher in endurance  
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14 287 than in power, team and non-athletes, which may be a consequence of effects of endurance training on  
15  
16 288 the respiratory muscles (Powers et al. 1997). Indeed, respiratory muscle training has been shown to  
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18 289 improve exercise performance in paraplegic athletes (Mueller et al. 2008) and the significance of  
19  
20 290 respiratory muscle training on performance is often underestimated in healthy people (Spengler and  
21  
22 291 Boutellier 2000). The high ventilation will help maintain oxygen saturation in the arterial blood, a real  
23  
24 292 challenge in endurance athletes, as increasing the pulmonary oxygen saturation by extra oxygen in the  
25  
26 293 inspired air improves their performance (Amann 2012), and the larger ventilation during exercise may  
27  
28 294 thus contribute to the larger  $VO_{2max}$  in endurance than power athletes.  
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### 33 34 35 296 *Anaerobic power*

36  
37  
38 297 Power and team athletes had the highest jumping power as we recently also observed in master athletes  
39  
40 298 (Bagley et al. 2019). Power is the product of force and velocity and in a previous study, the better  
41  
42 299 jumping performance in power than endurance athletes was attributed to faster contractile properties of  
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44 300 their muscles (Loturco et al. 2015). At first glance, our data appears to support this study, as the velocity  
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46 301 at take-off during a countermovement jump was higher in power and team than endurance and non-  
47  
48 302 athletes. However, the body mass as a proportion of maximal knee extension torque was lower in power  
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50 303 and team athletes than non-athletes and endurance athletes. According to the force-velocity relationship,  
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52 304 this lower body mass to maximal torque ratio will, independent of the contractile properties of the  
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54 305 muscle, result in a higher take-off velocity. If faster contractile properties play a role, then the velocity  
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56 306 at take-off at a given body mass to maximal torque ratio must be higher in power than endurance  
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2 307 athletes. Here we observed that the relationship between velocity at take-off and the ratio body mass to  
3 308 peak knee extension torque was similar between groups. The larger power of team and power athletes  
4 309 than non-athletes and endurance athletes is thus primarily attributable to the larger force generating  
5 310 capacity, and not faster contractile properties, of their muscles, a situation also seen in elite soccer  
6 311 players where jumping and sprinting performance were strongly associated with leg muscle strength  
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9 312 (Wisloff et al. 2004).

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17 314 *Aerobic to anaerobic power ratio*

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20 315 In line with previous observations in master athletes (Bagley et al. 2019), maximal aerobic power during  
21 316 an incremental exercise test was less than 15% of peak jump (anaerobic) power in all groups except in  
22 317 endurance athletes where it amounted to 21% of their maximal power. These values are higher than that  
23 318 observed in master athletes, but this could be due to cycling in the previous study rather than running  
24 319 to determine aerobic power and the higher age of the participants in that study. The potentially higher  
25 320 running economy in runners than in non-runners may have led to an underestimation of their aerobic  
26 321 power at VO<sub>2</sub>max in the treadmill-running test. If so, the ratio would be even higher in endurance  
27 322 athletes. It is unlikely, however, that such an underestimation explains the discrepancy between the 15-  
28 323 21% and the 30% of anaerobic power reported previously (Chamari et al. 1995). It is more likely that  
29 324 the discrepancy is attributable to the fact that Chamari et al. used cycle ergometry to determine  
30 325 anaerobic power, where muscles in each leg are alternately recruited during pedaling, in contrast to  
31 326 the simultaneous action of both legs in the countermovement jump in our study. Whatever the cause,  
32 327 even in endurance athletes the aerobic power represents a rather low proportion of the total muscle  
33 328 power available, and suggests there is a significant reserve capacity of anaerobic power.

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54 330 *Limitations.* This was a cross-sectional study and did not study the effects of specific training programs,  
55 331 where the differences between our groups may be to some extent attributable to genotypic differences  
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57 332 (Erskine et al. 2014; Hagberg et al. 2001) rather than different training programmes. We have lumped

1 333 participants of widely different sports together in the different athletic groups that will undoubtedly add  
2 334 to the variation within groups. For instance, power athletes included not only the slender sprinters, but  
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4 335 also agile wrestlers and bulky body builders that clearly require different adaptations to succeed in their  
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6 336 sport. Some of them trained primarily their upper body strength, while others trained lower or even  
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8 337 whole body strength and power. However, they are all characterized by the primary need to generate  
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10 338 large muscle power often explosively, and not endurance, and were therefore considered power athletes,  
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12 339 while endurance athletes were characterized by specialization in endurance events. In all athletic  
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14 340 groups, there was a vast range of performance levels. This is at the same time a strength of the study as  
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16 341 it ensures that the observations not only apply to top athletes, but also to those exercising at a high  
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18 342 recreational level. Finally, the determination of stroke volume at rest and not during exercise may have  
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20 343 underestimated the contribution of the continuing rise in stroke volume up to  $VO_{2max}$ , as seen in elite  
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22 344 endurance athletes (Zhou et al. 2001). If that also occurred in our endurance athletes, it means that our  
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24 345 conclusion that the larger oxygen pulse in endurance athletes reflects a higher oxygen extraction needs  
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26 346 to be treated with caution and deserves further investigation. However, this will have a minimal impact  
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28 347 on our data, as most participants were recreational athletes. Such athletes do not show such a continuing  
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30 348 rise in stroke volume during an incremental exercise test and, in line with our conclusion, exhibited a  
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32 349 larger oxygen extraction than non-athletes in that study (Zhou et al. 2001).  
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#### 41 351 *Perspective*

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44 352 The larger anaerobic (jumping) power in power than other athletes is largely attributable to their larger  
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46 353 muscle strength and not to faster contractile properties. Endurance athletes had a larger  $VO_{2max}$ , than  
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48 354 power athletes. The structural adaptations in terms of RWT, LV mass and stroke volume were similar  
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50 355 in all athletic groups. It is interesting to note that the  $VO_{2max}$  ( $L \cdot min^{-1}$ ) of team athletes was similar to  
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52 356 that of endurance athletes, and their power (W) was similar to that of power athletes, suggesting that  
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54 357 combined training does elicit the benefit of both exercise modalities. This suggests that adding heavy  
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56 358 resistance/plyometric and endurance training components to endurance and power athletes does not, in  
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58 359 contrast to what is expected from the Principle of Allocation, diminish their endurance and power  
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360 performance, respectively (Boullosa et al. 2013). This corresponds with our previous observations in  
361 animal muscle that the alleged trade-off between muscle fibre size and oxidative capacity can be broken  
362 (Omairi et al. 2016), and that muscle hypertrophy with a maintained muscle oxidative capacity is  
363 accompanied with increased fatigue resistance (Ballak et al. 2016).

364  
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487 **FIGURE LEGENDS**

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3 488 **Figure 1:** Maximal oxygen uptake in **A)**  $L \cdot \text{min}^{-1}$  and **B)**  $L \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ , and **C)** stroke volume per body  
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5 489 mass ( $\text{mL} \cdot \text{kg}^{-1}$ ) in non-athletes, endurance, power and team-playing athletes. <sup>a</sup>: different from control  
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7 490 at  $p \leq 0.002$ ; <sup>b</sup>: different from endurance athletes at  $p < 0.0005$ ; <sup>c</sup>: different from power athletes at  $p = 0.014$ .

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13 492 **Figure 2:** **A)** countermovement jumping power, **B)** maximal  $30^\circ \cdot \text{s}^{-1}$  knee extension torque, **C)**  
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15 493 velocity at take-off and **D)** the velocity at take-off versus body mass to maximal  $30^\circ \cdot \text{s}^{-1}$  knee  
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17 494 extension torque in non-athletes (white symbols), endurance (light grey symbols) athletes, power  
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19 495 (dark grey symbols) athletes and team (black symbols) athletes (pooled data:  $R^2 = 0.226$ ;  $p < 0.005$ ). <sup>a</sup>:  
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21 496 different from control; <sup>b</sup>: different from endurance athletes at  $p < 0.001$ .

498 **Table 1:** Characteristics, performance and cardiac parameters in Non-athletes, Endurance,  
 499 Power and Team athletes.

	Non-athletes	Endurance	Power	Team
Age (y)	24.5 ± 4.3 (207)	22.3 ± 3.6 (81) <sup>a</sup>	22.7 ± 3.5 (72) <sup>a</sup>	21.5 ± 3.1 (56) <sup>a</sup>
Height (m)	1.80 ± 0.06 (216)	1.79 ± 0.05 (86)	1.81 ± 0.06 (75)	1.87 ± 0.08 (58) <sup>a,b,c</sup>
Body mass (kg)	77.4 ± 11.0 (218)	70.5 ± 6.7 (85) <sup>a</sup>	81.5 ± 11.9 (72) <sup>a,b</sup>	80.8 ± 9.1 (59) <sup>b</sup>
Skinfolds (mm)	72.6 ± 43.2 (216)	33.9 ± 13.8 (86) <sup>a</sup>	56.1 ± 28.5 (75) <sup>a,b</sup>	48.6 ± 22.5 (59) <sup>a</sup>
BMI (kg·m <sup>-2</sup> )	23.8 ± 2.9 (215)	21.9 ± 1.7 (84) <sup>a</sup>	25.0 ± 2.8 (72) <sup>a,b</sup>	23.1 ± 1.5 (57) <sup>b,c</sup>
Shuttle run (s)	20.2 ± 1.3 (211)	19.6 ± 0.9 (85) <sup>a</sup>	19.7 ± 1.0 (73) <sup>a</sup>	19.7 ± 1.4 (50)
Jumping Power (W·kg <sup>-1</sup> )	26.5 ± 2.0 (212)	26.4 ± 2.0 (81)	28.3 ± 2.3 (72) <sup>a</sup>	28.1 ± 1.8 (57) <sup>a</sup>
BM/MVC (kg·Nm <sup>-1</sup> )	0.33 ± 0.05 (214)	0.31 ± 0.04 (78) <sup>a</sup>	0.29 ± 0.04 (72) <sup>a</sup>	0.29 ± 0.04 (53) <sup>a,b</sup>
Aerobic/Anaerobic (%)	14.0 ± 1.8 (182)	20.6 ± 3.4 (69) <sup>a</sup>	14.3 ± 2.8 (67) <sup>b</sup>	15.3 ± 2.3 (47) <sup>a,b</sup>
[Hb] (g·L <sup>-1</sup> )	151 ± 10 (217)	150 ± 12 (83)	152 ± 10 (75)	150 ± 9 (60)
HR (min <sup>-1</sup> )	197 ± 10 (150)	193 ± 9 (69)	196 ± 10 (62)	192 ± 9 (44)
LV mass (g)	181 ± 38 (217)	227 ± 48 (84) <sup>a</sup>	221 ± 45 (73) <sup>a</sup>	219 ± 46 (59) <sup>a</sup>
RWT	0.37 ± 0.05 (217)	0.40 ± 0.06 (84) <sup>a</sup>	0.40 ± 0.05 (73) <sup>a</sup>	0.38 ± 0.04 (59)
SV (mL)	87.9 ± 16.2 (216)	94.8 ± 15.0 (77) <sup>a</sup>	94.9 ± 17.7 (71) <sup>a</sup>	96.0 ± 14.8 (57) <sup>a</sup>
O <sub>2</sub> pulse/SV (mL·mL <sup>-1</sup> )	0.42 ± 0.09 (135)	0.46 ± 0.09 (62) <sup>a</sup>	0.42 ± 0.074 (62) <sup>b</sup>	0.44 ± 0.07 (39)
EF (%)	67.1 ± 4.5 (216)	67.0 ± 4.8 (80)	66.4 ± 5.6 (73)	66.8 ± 4.7 (59)

500 Values are mean ± SD; between parentheses number of individuals; BMI: body mass index;  
 501 BM/MVC: Body mass to maximal 30°·s<sup>-1</sup> knee extension torque; Aerobic/anaerobic: ratio of  
 502 power at VO<sub>2</sub>max to jumping power; [Hb]: Haemoglobin concentration; HR: maximal heart  
 503 rate; LV: left ventricle; RWT: Relative left cardiac ventricle wall thickness; EF: ejection  
 504 fraction (at rest); SV: stroke volume (at rest) <sup>a</sup>: different from non-athletes at p≤0.015; <sup>b</sup>:  
 505 different from endurance athletes at p<0.05; <sup>c</sup>: different from power athletes at p<0.005.

507 **Table 2:** Spirometry parameters in Non-athletes, Endurance, Power and Team athletes.

	Non-athletes	Endurance	Power	Team
5 $VE_{\max}$ (L·min <sup>-1</sup> )	146 ± 22 (186)	165 ± 23 (73) <sup>a</sup>	153 ± 23 (67) <sup>a</sup>	162 ± 18 (48) <sup>a</sup>
7 $VE_{\max}$ (L·kg <sup>-1</sup> ·min <sup>-1</sup> )	1.90 ± 0.28 (186)	2.36 ± 0.30 (73) <sup>a</sup>	1.91 ± 0.32 (67) <sup>b</sup>	2.01 ± 0.25 (41) <sup>b</sup>
9 $BF_{\max}$ (min <sup>-1</sup> )	58.0 ± 10.6 (186)	65.0 ± 10.8 (73) <sup>a</sup>	58.1 ± 9.3 (67) <sup>b</sup>	60.4 ± 9.4 (48)
11 $VT_{\max}$ (L)	3.01 ± 0.56 (186)	2.90 ± 0.44 (73)	3.03 ± 0.49 (67)	3.07 ± 0.55 (48)
13 $VT_{\max}/BM$ (mL·kg <sup>-1</sup> )	39 ± 7 (186)	42 ± 6 (73)	38 ± 6 (67) <sup>b</sup>	38 ± 5 (48) <sup>b</sup>
15 $FVC_{\text{pred}}$ (%)	99.2 ± 14.6 (211)	100.6 ± 13.4 (80)	101.7 ± 15.0 (71) <sup>a</sup>	109.0 ± 15.0 (56) <sup>a,b,c</sup>
17 $FEV_{1\text{pred}}$ (%)	107.0 ± 13.5 (211)	109.2 ± 13.2 (80) <sup>a</sup>	109.9 ± 12.4 (71)	116.2 ± 16.8 (56) <sup>a,b</sup>
19 $PEF_{\text{pred}}$ (%)	151 ± 10 (217)	150 ± 12 (83)	152 ± 10 (75)	150 ± 9 (60)

508 Values are mean ± SD; between parentheses number of individuals;  $VE_{\max}$ : Maximal exercise-  
 509 induced ventilation;  $BF_{\max}$ : Maximal exercise-induced breathing frequency;  $VT_{\max}$ : Maximal  
 510 exercise-induced tidal volume;  $VT_{\max}/BM$ :  $VT_{\max}$  per kg body mass; Maximal exercise-  
 511 induced tidal volume;  $FVC_{\text{pred}}$ : Predicted forced vital capacity;  $FEV_{1\text{pred}}$ : Predicted forced  
 512 expiratory volume in one second;  $PEF_{\text{pred}}$ : Predicted peak expiratory flow; <sup>a</sup>: different from  
 513 non-athletes; <sup>b</sup>: different from endurance; <sup>c</sup>: different from power at p≤0.032.

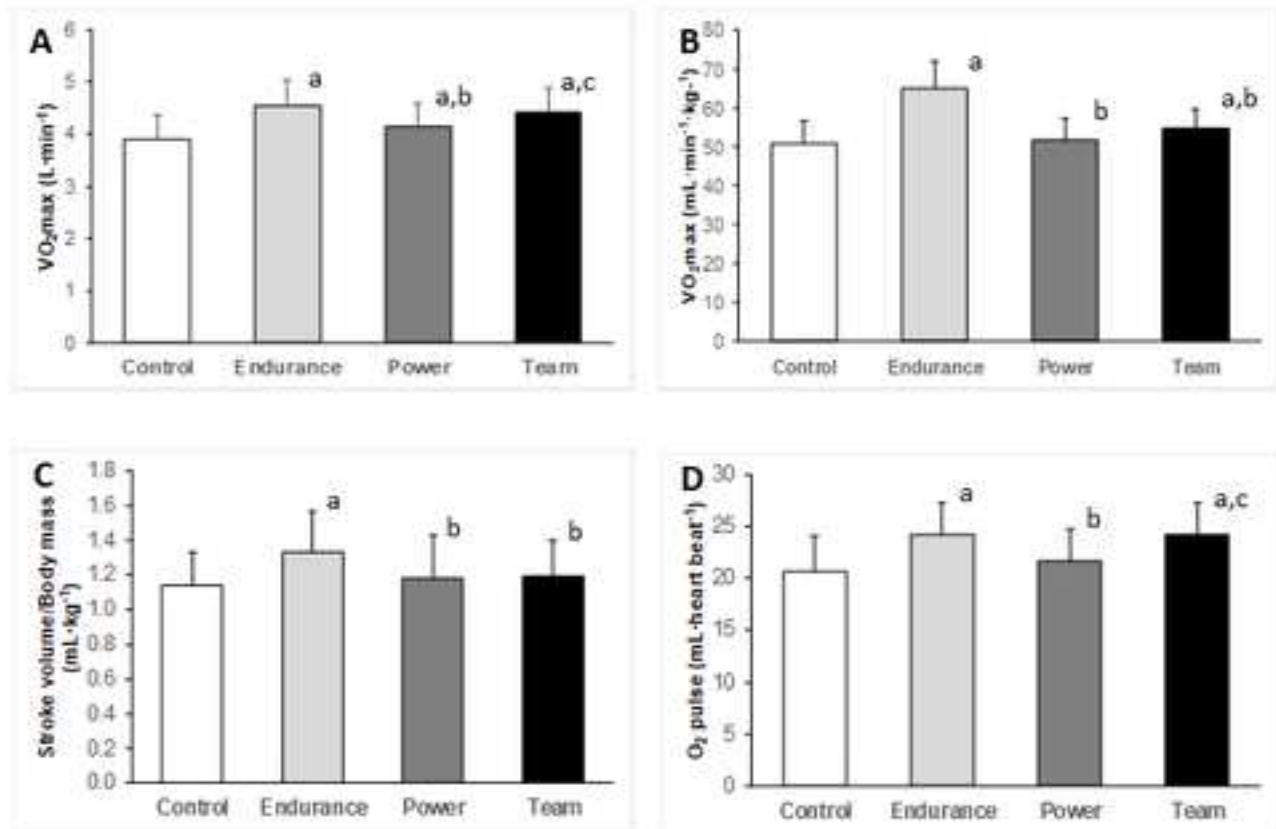


Figure 1 Degens et al

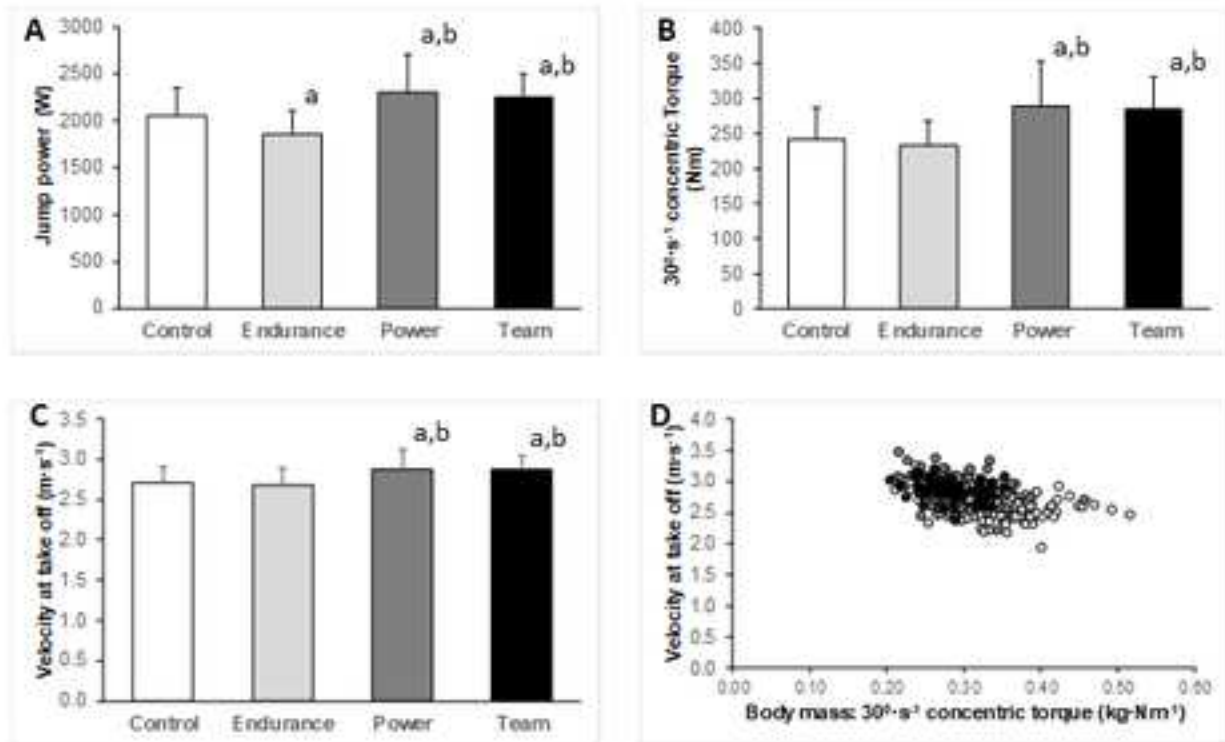


Figure 2 Degens et al



**Table 1:** Characteristics, performance and cardiac parameters in Non-athletes, Endurance, Power and Team athletes.

	Non-athletes	Endurance	Power	Team
Age (y)	24.5 ± 4.3 (207)	22.3 ± 3.6 (81) <sup>a</sup>	22.7 ± 3.5 (72) <sup>a</sup>	21.5 ± 3.1 (56) <sup>a</sup>
Height (m)	1.80 ± 0.06 (216)	1.79 ± 0.05 (86)	1.81 ± 0.06 (75)	1.87 ± 0.08 (58) <sup>a,b,c</sup>
Body mass (kg)	77.4 ± 11.0 (218)	70.5 ± 6.7 (85) <sup>a</sup>	81.5 ± 11.9 (72) <sup>a,b</sup>	80.8 ± 9.1 (59) <sup>b</sup>
Skinfolds (mm)	72.6 ± 43.2 (216)	33.9 ± 13.8 (86) <sup>a</sup>	56.1 ± 28.5 (75) <sup>a,b</sup>	48.6 ± 22.5 (59) <sup>a</sup>
BMI (kg·m <sup>-2</sup> )	23.8 ± 2.9 (215)	21.9 ± 1.7 (84) <sup>a</sup>	25.0 ± 2.8 (72) <sup>a,b</sup>	23.1 ± 1.5 (57) <sup>b,c</sup>
Shuttle run (s)	20.2 ± 1.3 (211)	19.6 ± 0.9 (85) <sup>a</sup>	19.7 ± 1.0 (73) <sup>a</sup>	19.7 ± 1.4 (50)
Jumping Power (W·kg <sup>-1</sup> )	26.5 ± 2.0 (212)	26.4 ± 2.0 (81)	28.3 ± 2.3 (72) <sup>a</sup>	28.1 ± 1.8 (57) <sup>a</sup>
BM/MVC (kg·Nm <sup>-1</sup> )	0.33 ± 0.05 (214)	0.31 ± 0.04 (78) <sup>a</sup>	0.29 ± 0.04 (72) <sup>a</sup>	0.29 ± 0.04 (53) <sup>a,b</sup>
Aerobic/Anaerobic (%)	14.0 ± 1.8 (182)	20.6 ± 3.4 (69) <sup>a</sup>	14.3 ± 2.8 (67) <sup>b</sup>	15.3 ± 2.3 (47) <sup>a,b</sup>
[Hb] (g·L <sup>-1</sup> )	151 ± 10 (217)	150 ± 12 (83)	152 ± 10 (75)	150 ± 9 (60)
HR (min <sup>-1</sup> )	197 ± 10 (150)	193 ± 9 (69)	196 ± 10 (62)	192 ± 9 (44)
LV mass (g)	181 ± 38 (217)	227 ± 48 (84) <sup>a</sup>	221 ± 45 (73) <sup>a</sup>	219 ± 46 (59) <sup>a</sup>
RWT	0.37 ± 0.05 (217)	0.40 ± 0.06 (84) <sup>a</sup>	0.40 ± 0.05 (73) <sup>a</sup>	0.38 ± 0.04 (59)
SV (mL)	87.9 ± 16.2 (216)	94.8 ± 15.0 (77) <sup>a</sup>	94.9 ± 17.7 (71) <sup>a</sup>	96.0 ± 14.8 (57) <sup>a</sup>
O <sub>2</sub> pulse/SV (mL·mL <sup>-1</sup> )	0.42 ± 0.09 (135)	0.46 ± 0.09 (62) <sup>a</sup>	0.42 ± 0.074 (62) <sup>b</sup>	0.44 ± 0.07 (39)
EF (%)	67.1 ± 4.5 (216)	67.0 ± 4.8 (80)	66.4 ± 5.6 (73)	66.8 ± 4.7 (59)

Values are mean ± SD; between parentheses number of individuals; BMI: body mass index; BM/MVC: Body mass to maximal 30°·s<sup>-1</sup> knee extension torque; Aerobic/anaerobic: ratio of power at VO<sub>2</sub>max to jumping power; [Hb]: Haemoglobin concentration; HR: maximal heart rate; LV: left ventricle; RWT: Relative left cardiac ventricle wall thickness; EF: ejection fraction (at rest); SV: stroke volume (at rest) <sup>a</sup>: different from non-athletes at p≤0.015; <sup>b</sup>: different from endurance athletes at p<0.05; <sup>c</sup>: different from power athletes at p<0.005.

**Table 2:** Spirometry parameters in Non-athletes, Endurance, Power and Team athletes.

	Non-athletes	Endurance	Power	Team
$VE_{\max}$ (L·min <sup>-1</sup> )	146 ± 22 (186)	165 ± 23 (73) <sup>a</sup>	153 ± 23 (67) <sup>a</sup>	162 ± 18 (48) <sup>a</sup>
$VE_{\max}$ (L·kg <sup>-1</sup> ·min <sup>-1</sup> )	1.90 ± 0.28 (186)	2.36 ± 0.30 (73) <sup>a</sup>	1.91 ± 0.32 (67) <sup>b</sup>	2.01 ± 0.25 (41) <sup>b</sup>
$BF_{\max}$ (min <sup>-1</sup> )	58.0 ± 10.6 (186)	65.0 ± 10.8 (73) <sup>a</sup>	58.1 ± 9.3 (67) <sup>b</sup>	60.4 ± 9.4 (48)
$VT_{\max}$ (L)	3.01 ± 0.56 (186)	2.90 ± 0.44 (73)	3.03 ± 0.49 (67)	3.07 ± 0.55 (48)
$VT_{\max}/BM$ (mL·kg <sup>-1</sup> )	39 ± 7 (186)	42 ± 6 (73)	38 ± 6 (67) <sup>b</sup>	38 ± 5 (48) <sup>b</sup>
$FVC_{\text{pred}}$ (%)	99.2 ± 14.6 (211)	100.6 ± 13.4 (80)	101.7 ± 15.0 (71) <sup>a</sup>	109.0 ± 15.0 (56) <sup>a,b,c</sup>
$FEV_{1\text{pred}}$ (%)	107.0 ± 13.5 (211)	109.2 ± 13.2 (80) <sup>a</sup>	109.9 ± 12.4 (71)	116.2 ± 16.8 (56) <sup>a,b</sup>
$PEF_{\text{pred}}$ (%)	151 ± 10 (217)	150 ± 12 (83)	152 ± 10 (75)	150 ± 9 (60)

Values are mean ± SD; between parentheses number of individuals;  $VE_{\max}$ : Maximal exercise-induced ventilation;  $BF_{\max}$ : Maximal exercise-induced breathing frequency;  $VT_{\max}$ : Maximal exercise-induced tidal volume;  $VT_{\max}/BM$ :  $VT_{\max}$  per kg body mass; Maximal exercise-induced tidal volume;  $FVC_{\text{pred}}$ : Predicted forced vital capacity;  $FEV_{1\text{pred}}$ : Predicted forced expiratory volume in one second;  $PEF_{\text{pred}}$ : Predicted peak expiratory flow; <sup>a</sup>: different from non-athletes; <sup>b</sup>: different from endurance; <sup>c</sup>: different from power at  $p \leq 0.032$ .

Author contribution statement

H.D., A.S., A.S, B.S., and T.V. conceived the study and collected the data. H.D. and T.V. performed the analyses. All authors discussed the results and contributed to the writing of the manuscript.