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Abstract

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

Endurance ($n=87$; distance runners, road cyclists, paddlers, skiers), power ($n=77$; sprinters, throwers, combat sport athletes, body builders), team ($n=64$; basketball, soccer, volleyball) and non-athletes ($n=223$) performed a countermovement jump and an incremental running test to estimate their maximal anaerobic and aerobic power (VO_2max), respectively. Dynamometry and M-mode echocardiography were used to measure muscle strength and stroke volume. The VO_2max ($\text{L}\cdot\text{min}^{-1}$) was larger in endurance and team athletes than in power athletes and non-athletes ($p<0.05$). Athletes had a larger stroke volume, left ventricular mass and left ventricular wall thickness than non-athletes ($p<0.02$), but there were no significant differences between athlete groups. The higher anaerobic power in power and team athletes than in endurance athletes and non-athletes ($p<0.001$) was associated with a larger force ($p<0.001$), but not faster contractile properties. Endurance athletes (20.6%) had a higher ($p<0.05$) aerobic:anaerobic power ratio than controls and power and team athletes (14.0-15.3%). The larger oxygen pulse, without significant differences in stroke volume, in endurance than power athletes indicates a larger oxygen extraction during exercise. Power athletes had stronger, but not faster, muscles than endurance athletes. The similar VO_2max in endurance and team athletes and similar jump power in team and power athletes, suggests that concurrent training does not necessarily impair power or 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; $VO_{2\max}$, maximal oxygen uptake; VT_{\max} , tidal volume.

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Introduction

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

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

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

implying that many athletes perform well in both endurance and power events in the decathlon. Further support for the notion that power and endurance can go together comes from athletes that excel in both sprinting and long distance running (Eynon et al. 2011). Finally, the maximal oxygen uptake ($VO_2\text{max}$) of endurance athletes is not negatively affected by additional resistance exercise, and endurance performance may even improve (Hickson et al. 1988; Vikmoen et al. 2016; Boullosa et al. 2013). In fact, resistance and power training can also increase stroke volume and $VO_2\text{max}$ (Kraemer et al. 1988; Venckunas et al. 2011). Furthermore, we previously observed that there were no significant differences in the ventilatory function of master power and endurance athletes (Degens et al. 2013). While endurance and resistance training are considered to elicit different physiological adaptations, these observations suggest that there is no strict dichotomy between power and endurance athletes.

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

Methods

Study design

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

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

Shuttle run test

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

Countermovement jump

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

$$v = a * t_f/2$$

where ‘a’ is the gravitational acceleration (9.81 m·s⁻²) and ‘t_f’ the flight time of the jump. The flight time was the time from take-off (no force recorded on the platform) until landing (the moment that forces on the platform are registered again). The power (in Watts) of the countermovement jump was given as an estimate of Maximal Anaerobic Power and calculated as:

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

Maximal voluntary contraction

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

Maximal incremental exercise test

To measure VO₂max, a ramp treadmill (H/P/Cosmos Sports & Medical GMBH, Germany) protocol of continuous incremental running speed until exhaustion was applied. The participants started the test by jogging at 7 km·h⁻¹ for 3 min at an initial gradient of 1%, and then the speed of the treadmill belt increased by 0.1 km·h⁻¹ every 6 seconds. When the treadmill speed reached 20 km·h⁻¹ the speed was not increased further, but the gradient of the treadmill was increased by 0.05% every 6 s. Throughout the test, breath-by-breath gas analysis was performed using an Oxycon Mobile gas analyzer (Viasys, Germany), and heart rate (HR) was recorded with a HR meter 810s (Polar, Finland). VO₂max was considered to be reached when the heart rate reached >90% predicted maximal heart rate, the respiratory exchange ratio (RER) was > 1.1 and the participant could not continue running at the required pace

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

Aerobic:anaerobic power ratio

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

Spirometry

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

Cardiac parameters

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

approximately 75% increase in SV during exercise (Zhou et al. 2001)), giving the VO_2 per SV ($\text{mL O}_2 \cdot \text{mL}^{-1}$) during maximal exercise.

Since hemoglobin is the main carrier of oxygen, a finger-prick blood sample was taken to determine the hemoglobin concentration in a ClinCheckAlpha (Biochemical Systems International, Arezzo, Italy).

Statistics

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

$$\text{CV} = 100 * \text{SD}_{\text{dif}} * \mu$$

where SD_{dif} represents the standard deviation of the difference between repeated measurements and μ represents the mean of the pooled test-retest data.

ANOVA with a Bonferroni-corrected post-hoc test was used to assess differences between groups. The Shapiro-Wilk test showed that the data were normally distributed. Pearson correlation coefficients represented relationships between parameters. Differences were considered significant at $p < 0.05$. Descriptive data is shown as mean \pm SD.

Results

The CVs were: maximal heart rate 2.5%, left ventricular mass 17.6%, SV 9.5%, %EF 8.4%, VE_{max} 9.1%, VT_{max} 11.2%, BF_{max} 12.6%, $\text{VO}_{2\text{max}}$ 8.8%.

Non-athletes were on average 2 years older than athletes ($p < 0.001$; Table 1). The body mass and BMI were lowest in endurance athletes ($p < 0.05$) and higher in power athletes than in non-athletes ($p < 0.001$). While team athletes were taller than participants in all other groups ($p < 0.001$), their body mass and BMI did not differ significantly from non-athletes. The sum of the skinfold thicknesses was smaller in

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).

The VO_2max in $\text{L}\cdot\text{min}^{-1}$ of athletes was higher than that of non-athletes ($p\leq 0.002$), where endurance and team athletes had a higher VO_2max than power athletes ($p\leq 0.014$; Fig 1A). VO_2max normalized to body mass was higher in endurance athletes than in any other group ($p<0.001$), but the difference between power athletes and non-athletes had disappeared (Fig. 1B).

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

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

Non-athletes achieved the least ($p<0.001$) and endurance athletes the highest ($p\leq 0.034$) maximal power during the progressive VO_2max test (Table 1).

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

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

VO_2max ($\text{mL} \cdot \text{min}^{-1}$) correlated positively with stroke volume ($R^2 = 0.16$; $p < 0.001$). The velocity at take-off correlated inversely with the body mass: maximal $30^\circ \cdot \text{s}^{-1}$ knee extension torque ratio ($R^2 = 0.226$; $p < 0.001$; Figure 2D) and this ratio was lower in athletes than non-athletes ($p \leq 0.008$) and lower in team than endurance athletes ($p = 0.032$; Table 1).

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

There were no significant relationships between the performance in the shuttle run test with VO_2max , maximal $30^\circ \cdot \text{s}^{-1}$ knee extension torque or maximal jumping power per body mass (data not shown).

Discussion

The main observation of the present study is that the larger anaerobic (jumping) power of power and team athletes than endurance and non-athletes is largely attributable to their larger muscle strength, and not to faster muscle contractile properties. The power at VO_2max is only about 21% of anaerobic power in endurance athletes and just 15% in non-athletes and power athletes. The higher oxygen pulse in endurance and team athletes than power athletes, and similar hemoglobin concentrations and stroke volumes, left ventricular mass and wall thickness, suggest that the endurance and team athletes realized part of their larger VO_2max via enhanced oxygen extraction. The observation that team athletes had a similar VO_2max to endurance athletes and a similar jump power as power athletes suggests that at least in our population superimposing regular resistance training to an endurance program or *vice versa* will not reduce performance in power events at the expense of endurance and *vice versa*.

Shuttle run test

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

Aerobic power

In all athletic groups the VO_2max in $\text{L}\cdot\text{min}^{-1}$ was higher than in non-athletes, with power athletes having a lower VO_2max than team and endurance athletes, something also seen previously (Bassett and Howley 2000; Bagley et al. 2019). The larger stroke volume in athletes than non-athletes undoubtedly contributes to their higher VO_2max , but this does not explain the difference in VO_2max between athlete groups as they all had a similar stroke volumes, at least at rest. These observations challenge the idea that resting stroke volume differs between endurance and power training (Fagard 2003) and with the similar left ventricular mass and wall thickness indicate that cardiac adaptations are similar in endurance and power athletes. The larger VO_2max in endurance than power athletes has therefore to be explained by other factors than differences in structural cardiac adaptations, such as a larger oxygen carrying capacity and/or oxygen extraction by endurance athletes. All groups had a similar [Hb] indicating a similar oxygen carrying capacity of the blood. The stroke volume at rest did not differ significantly between power and endurance athletes. If we assume that the stroke volume increases similarly during exercise, as seen in trained and untrained people, except for elite endurance athletes (Zhou et al. 2001), it suggests that the oxygen extraction from the blood was higher in endurance and team than in power athletes. Indeed, it has been suggested that the VO_2max during whole body exercise is primarily determined by the oxygen transport capacity and to a lesser extent by peripheral factors (capillary transfer and mitochondrial volume), even after endurance training, but the significance of the peripheral factors may increase with endurance training (di Prampero and Ferretti 1990). Indeed, an increased

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

Although spirometry did not differ much between athletes and non-athletes, as we have seen before in master athletes (Degens et al. 2013), the maximal exercise-induced ventilation was higher in endurance than in power, team and non-athletes, which may be a consequence of effects of endurance training on the respiratory muscles (Powers et al. 1997). Indeed, respiratory muscle training has been shown to improve exercise performance in paraplegic athletes (Mueller et al. 2008) and the significance of respiratory muscle training on performance is often underestimated in healthy people (Spengler and Boutellier 2000). The high ventilation will help maintain oxygen saturation in the arterial blood, a real challenge in endurance athletes, as increasing the pulmonary oxygen saturation by extra oxygen in the inspired air improves their performance (Amann 2012), and the larger ventilation during exercise may thus contribute to the larger VO_2max in endurance than power athletes.

Anaerobic power

Power and team athletes had the highest jumping power as we recently also observed in master athletes (Bagley et al. 2019). Power is the product of force and velocity and in a previous study, the better jumping performance in power than endurance athletes was attributed to faster contractile properties of their muscles (Loturco et al. 2015). At first glance, our data appears to support this study, as the velocity at take-off during a countermovement jump was higher in power and team than endurance and non-athletes. However, the body mass as a proportion of maximal knee extension torque was lower in power and team athletes than non-athletes and endurance athletes. According to the force-velocity relationship, this lower body mass to maximal torque ratio will, independent of the contractile properties of the muscle, result in a higher take-off velocity. If faster contractile properties play a role, then the velocity at take-off at a given body mass to maximal torque ratio must be higher in power than endurance

athletes. Here we observed that the relationship between velocity at take-off and the ratio body mass to peak knee extension torque was similar between groups. The larger power of team and power athletes than non-athletes and endurance athletes is thus primarily attributable to the larger force generating capacity, and not faster contractile properties, of their muscles, a situation also seen in elite soccer players where jumping and sprinting performance were strongly associated with leg muscle strength (Wisloff et al. 2004).

Aerobic to anaerobic power ratio

In line with previous observations in master athletes (Bagley et al. 2019), maximal aerobic power during an incremental exercise test was less than 15% of peak jump (anaerobic) power in all groups except in endurance athletes where it amounted to 21% of their maximal power. These values are higher than that observed in master athletes, but this could be due to cycling in the previous study rather than running to determine aerobic power and the higher age of the participants in that study. The potentially higher running economy in runners than in non-runners may have led to an underestimation of their aerobic power at $\text{VO}_{2\text{max}}$ in the treadmill-running test. If so, the ratio would be even higher in endurance athletes. It is unlikely, however, that such an underestimation explains the discrepancy between the 15-21% and the 30% of anaerobic power reported previously (Chamari et al. 1995). It is more likely that the discrepancy is attributable to the fact that Chamari et al. used cycle ergometry to determine anaerobic power, where muscles in each leg are alternately recruited during pedaling, in contrast to the simultaneous action of both legs in the countermovement jump in our study. Whatever the cause, even in endurance athletes the aerobic power represents a rather low proportion of the total muscle power available, and suggests there is a significant reserve capacity of anaerobic power.

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

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

Perspective

The larger anaerobic (jumping) power in power than other athletes is largely attributable to their larger muscle strength and not to faster contractile properties. Endurance athletes had a larger VO_{2max} , than power athletes. The structural adaptations in terms of RWT, LV mass and stroke volume were similar in all athletic groups. It is interesting to note that the VO_{2max} ($L \cdot min^{-1}$) of team athletes was similar to that of endurance athletes, and their power (W) was similar to that of power athletes, suggesting that combined training does elicit the benefit of both exercise modalities. This suggests that adding heavy resistance/plyometric and endurance training components to endurance and power athletes does not, in contrast to what is expected from the Principle of Allocation, diminish their endurance and power

performance, respectively (Boullosa et al. 2013). This corresponds with our previous observations in animal muscle that the alleged trade-off between muscle fibre size and oxidative capacity can be broken (Omairi et al. 2016), and that muscle hypertrophy with a maintained muscle oxidative capacity is accompanied with increased fatigue resistance (Ballak et al. 2016).

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FIGURE LEGENDS

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

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

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) ^a	22.7 ± 3.5 (72) ^a	21.5 ± 3.1 (56) ^a
Height (m)	1.80 ± 0.06 (216)	1.79 ± 0.05 (86)	1.81 ± 0.06 (75)	1.87 ± 0.08 (58) ^{a,b,c}
Body mass (kg)	77.4 ± 11.0 (218)	70.5 ± 6.7 (85) ^a	81.5 ± 11.9 (72) ^{a,b}	80.8 ± 9.1 (59) ^b
Skinfolds (mm)	72.6 ± 43.2 (216)	33.9 ± 13.8 (86) ^a	56.1 ± 28.5 (75) ^{a,b}	48.6 ± 22.5 (59) ^a
BMI (kg·m ⁻²)	23.8 ± 2.9 (215)	21.9 ± 1.7 (84) ^a	25.0 ± 2.8 (72) ^{a,b}	23.1 ± 1.5 (57) ^{b,c}
Shuttle run (s)	20.2 ± 1.3 (211)	19.6 ± 0.9 (85) ^a	19.7 ± 1.0 (73) ^a	19.7 ± 1.4 (50)
Jumping Power (W·kg ⁻¹)	26.5 ± 2.0 (212)	26.4 ± 2.0 (81)	28.3 ± 2.3 (72) ^a	28.1 ± 1.8 (57) ^a
BM/MVC (kg·Nm ⁻¹)	0.33 ± 0.05 (214)	0.31 ± 0.04 (78) ^a	0.29 ± 0.04 (72) ^a	0.29 ± 0.04 (53) ^{a,b}
Aerobic/Anaerobic (%)	14.0 ± 1.8 (182)	20.6 ± 3.4 (69) ^a	14.3 ± 2.8 (67) ^b	15.3 ± 2.3 (47) ^{a,b}
[Hb] (g·L ⁻¹)	151 ± 10 (217)	150 ± 12 (83)	152 ± 10 (75)	150 ± 9 (60)
HR (min ⁻¹)	197 ± 10 (150)	193 ± 9 (69)	196 ± 10 (62)	192 ± 9 (44)
LV mass (g)	181 ± 38 (217)	227 ± 48 (84) ^a	221 ± 45 (73) ^a	219 ± 46 (59) ^a
RWT	0.37 ± 0.05 (217)	0.40 ± 0.06 (84) ^a	0.40 ± 0.05 (73) ^a	0.38 ± 0.04 (59)
SV (mL)	87.9 ± 16.2 (216)	94.8 ± 15.0 (77) ^a	94.9 ± 17.7 (71) ^a	96.0 ± 14.8 (57) ^a
O ₂ pulse/SV (mL·mL ⁻¹)	0.42 ± 0.09 (135)	0.46 ± 0.09 (62) ^a	0.42 ± 0.074 (62) ^b	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⁻¹ knee extension torque; Aerobic/anaerobic: ratio of power at VO₂max 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) ^a: different from non-athletes at p≤0.015; ^b: different from endurance athletes at p<0.05; ^c: 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 ⁻¹)	146 ± 22 (186)	165 ± 23 (73) ^a	153 ± 23 (67) ^a	162 ± 18 (48) ^a
VE _{max} (L·kg ⁻¹ ·min ⁻¹)	1.90 ± 0.28 (186)	2.36 ± 0.30 (73) ^a	1.91 ± 0.32 (67) ^b	2.01 ± 0.25 (41) ^b
BF _{max} (min ⁻¹)	58.0 ± 10.6 (186)	65.0 ± 10.8 (73) ^a	58.1 ± 9.3 (67) ^b	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 ⁻¹)	39 ± 7 (186)	42 ± 6 (73)	38 ± 6 (67) ^b	38 ± 5 (48) ^b
FVC _{pred} (%)	99.2 ± 14.6 (211)	100.6 ± 13.4 (80)	101.7 ± 15.0 (71) ^a	109.0 ± 15.0 (56) ^{a,b,c}
FEV _{1pred} (%)	107.0 ± 13.5 (211)	109.2 ± 13.2 (80) ^a	109.9 ± 12.4 (71)	116.2 ± 16.8 (56) ^{a,b}
PEF _{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_{pred}: Predicted forced vital capacity; FEV_{1pred}: Predicted forced expiratory volume in one second; PEF_{pred}: Predicted peak expiratory flow; ^a: different from non-athletes; ^b: different from endurance; ^c: different from power at p≤0.032.

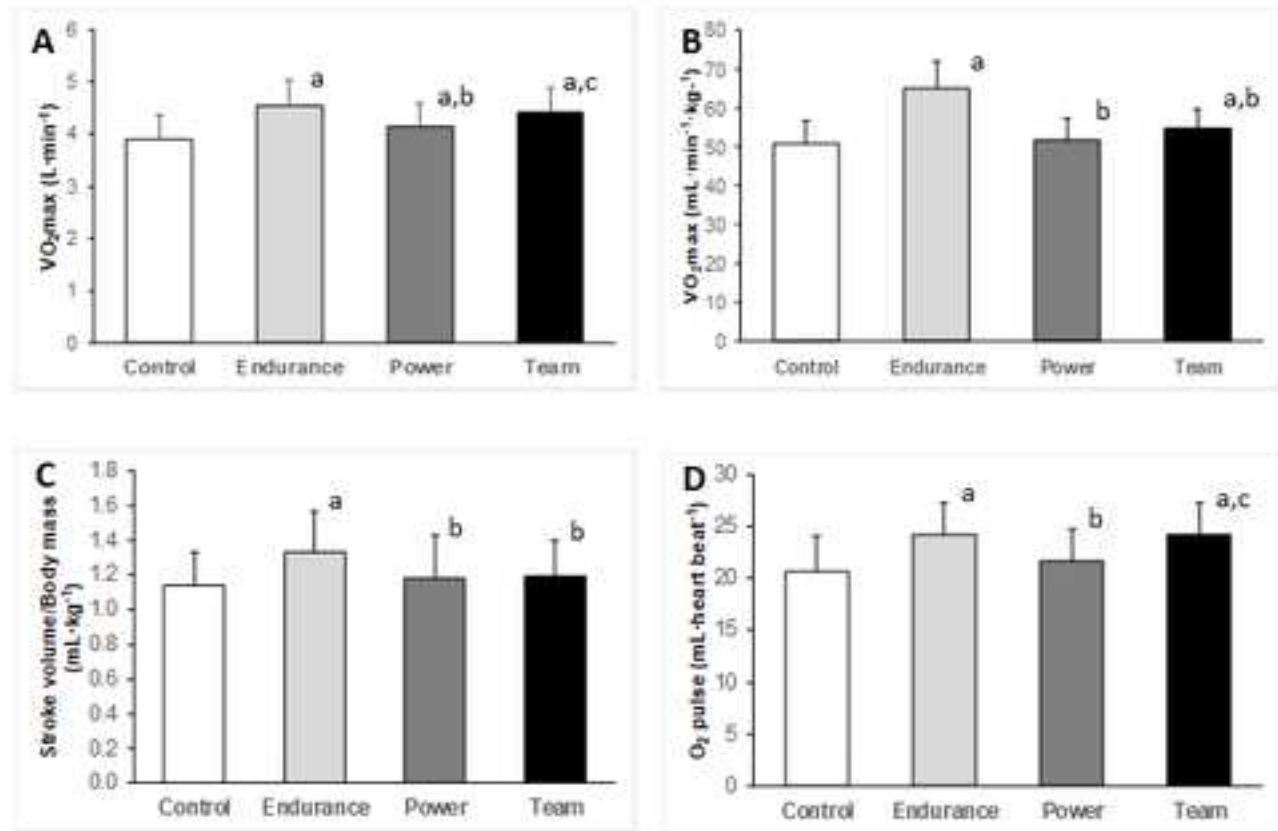


Figure 1 Degens et al

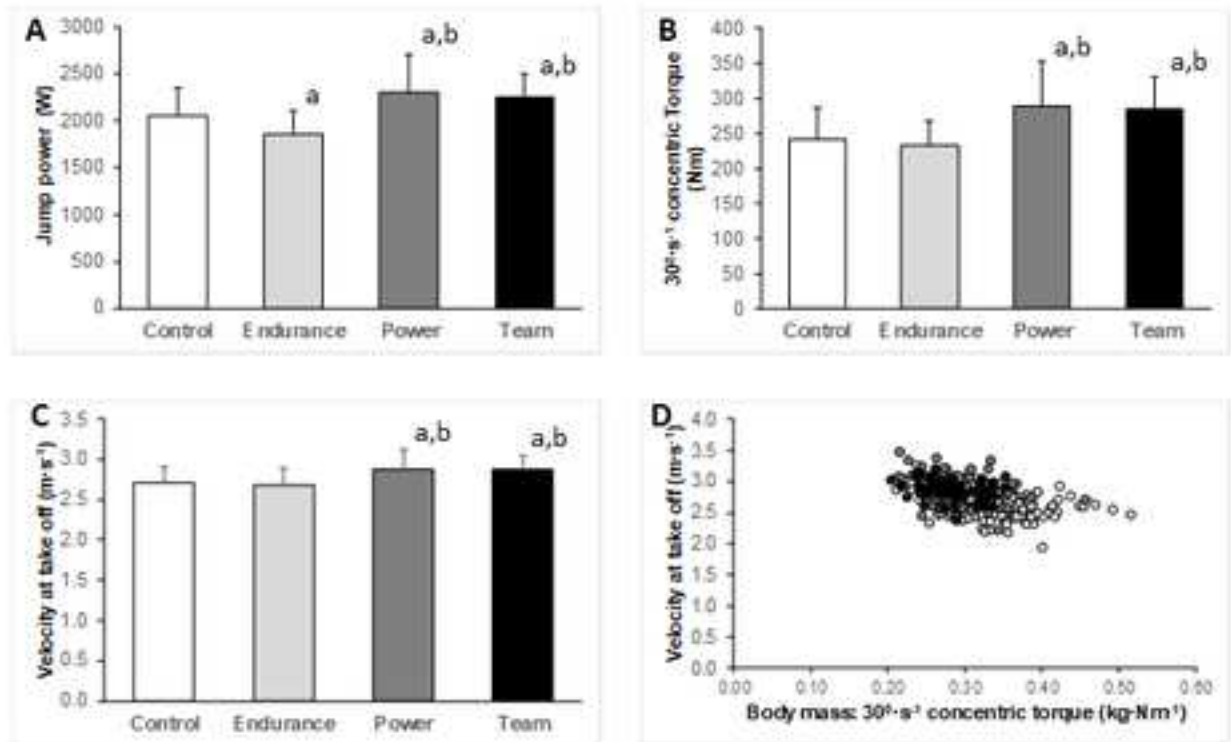


Figure 2 Degens et al

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

	Non-athletes	Endurance	Power	Team
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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.