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BODY MASS AND $V'O_2$ AT REST AFFECT GROSS EFFICIENCY DURING MODERATE-INTENSITY CYCLING IN UNTRAINED YOUNG HEALTHY MEN: CORRELATIONS WITH $V'O_{2MAX}$

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Seventeen young healthy physically active males (age 23 ±3 years; body mass (BM) 72.5 ±7.9 kg; height 178 ±4 cm, (mean ±SD)), not specifically trained in cycling, participated in this study. The subjects performed two cycling incremental tests at the pedalling rate of 60 rev·min^{-1}. The first test, with the power output (PO) increases of 30 W every 3 min, was to determine the maximal oxygen uptake ($V'O_{2max}$) and the power output (PO) at $V'O_{2max}$, while the second test (series of 6 minutes bouts of increasing intensity) was to determine energy expenditure (EE ($V'O_2$)), gross efficiency (GE ($V'O_2$/PO)) and delta efficiency (DE($\Delta V'O_2/\Delta PO$)) during sub-lactate threshold (LT) PO. $V'O_{2max}$ was 3.79 ±0.40 L·min^{-1} and the PO at $V'O_{2max}$ was 288 ±27 W. In order to calculate GE and DE the $V'O_2$ was expressed in W, by standard calculations. GE measured at 30 W, 60 W, 90 W and 120 W was 11.6 ±1.4%, 17.0 ±1.4%, 19.6 ±1.2% and 21.4 ±1.1%, respectively. DE was 29.8 ±1.9%. The subjects' BM (range 59–87 kg) was positively correlated with $V'O_2$ at rest ($p<0.01$) and with the intercept of the linear $V'O_2$ vs. PO relationship ($p<0.01$), whereas no correlation was found between BM and the slope of $V'O_2$ vs. PO. No correlation was found between BM and DE, whereas GE was negatively correlated with BM ($p<0.01$). GE was also negatively correlated with $V'O_{2max}$ and the PO at $V'O_{2max}$ ($p<0.01$). We conclude that: $V'O_2$ at rest affects GE during moderate-intensity cycling and GE negatively corelates with $V'O_{2max}$ and the PO at $V'O_{2max}$ in young healthy men.

Key words: *exercise, delta efficiency, gross efficiency, muscle efficiency, maximal oxygen uptake, power output, energy expenditure, lactate threshold, body mass index*

INTRODUCTION

Muscle efficiency is commonly expressed as the ratio of mechanical power output to the rate of metabolic energy expenditure (1-4). Whereas mechanical power output can be relatively easily measured, using various types of ergometers, the assessment of the rate of energy expenditure (EE) by the working muscle, especially at high exercise intensities, is far more complex, mainly as a consequence of the lack of methods allowing to quantify, *in vivo*, the contribution of phosphocreatine hydrolysis and anaerobic glycolysis-glycogenolysis (3, 5, 6). In order to simplify the assessment of the rate of EE during exercise, studies of mechanical efficiency during cycling are commonly limited to exercise of moderate intensity (*i.e.,* sub-lactate threshold intensities), which are performed under aerobic conditions, during which oxidative phosphorylation can be considered, as a first approximation, the only supplier of the ATP in the working muscles in steady-state conditions, that is after the initial rest-to-exercise metabolic transition (3, 7 ,8).

In the moderate exercise intensity domain the EE by the working muscles can be easily and precisely determined by measuring pulmonary $V'O_2$, which can then be expressed as Joules·min^{-1} assuming an energy equivalent of 20.9 kJ·L^{-1} of $V'O_2$ (after correction for the gas exchange ratio, R), and then in watts (W), following the equivalence of 1(W) = 1(J·s^{-1}), (1-3, 9). By doing so, having both the numerator (mechanical power output) and the denominator (metabolic energy expenditure) of the equation expressed in watts, allows efficiency to be expressed as a simple percentage. It should be also mentioned that, as shown by Poole *et al.* (10) the slope of the $V'O_2$ vs. PO relationship during cycling, based on the $V'O_2$ measured across muscles of the working legs (muscle $V'O_2$) was not different from that measured at the mouth (pulmonary $V'O_2$), amounting to 9.2 mL·min^{-1}·W^{-1} vs. 9.9 mL·min^{-1}·W^{-1}, respectively. Thus, pulmonary $V'O_2$ rate of increase measured during cycling rather closely reflects muscle $V'O_2$ rate of increase attributable to the PO rate of increase.

Several definitions of muscle efficiency have been utilized in the literature (2): 'gross' efficiency (GE) = mechanical work output/energy expenditure; 'net' efficiency = mechanical work output/energy expenditure above rest; 'work' efficiency = mechanical work output/energy expenditure above that corresponding to unloaded pedalling; 'delta' efficiency (DE) = Δ mechanical work output/Δ energy expenditure. Those that currently receive most attention are the concepts of GE and DE

(4). GE is simply expressed as the ratio between the mechanical work performed and the total body energy expenditure. In the case of DE a change in mechanical power output is at the nominator and the corresponding change in pulmonary $V'O_2$ is at the denominator. In case of GE assessment, the total $V'O_2$ used for its calculation includes three components: (i) resting metabolic rate, (ii) the cost of unloaded cycling ('internal work') and (iii) the cost of generation of a given external power output. Only the third component is considered in the calculation of DE.

An improvement of muscle mechanical efficiency during exercise leads to an increase of the mechanical power generating capabilities at a given $V'O_2$ (~ATP turnover), which is relevant both in case of athletes and in case of patients, independently from $V'O_{2max}$ (4, 11, 12). Studies concerning the factors determining mechanical efficiency during cycling attracted attention of many researchers, dating back to the beginning of the previous century (13) until now (2, 4, 10, 12, 14-16). Muscle efficiency can be modified by: (i) factors determining the ATP cost of force generation (ATP_{COST}) or/and (ii) the efficiency of mitochondrial ATP synthesis (ATP_{OX}) (7, 8, 17-20).

Among the factors which can influence muscle efficiency in humans (4, 7, 17, 18, 21, 22) during cycling is body mass (23), although the underlying mechanism is still unclear. According to Cotes (24), the $V'O_2$ at a given power output during cycling is greater in 'heavy' than in the 'light' subjects. This finding was confirmed by Wasserman and Whipp (25), who have shown that the O_2 requirement to perform cycling of a given intensity in obese subjects is shifted upward, when compared to people with a normal body mass. This important message, however, for a long time has not been transferred to the GE assessment in humans. This was probably caused by the general notion, coming from earlier influential studies, claiming that body mass has no effect on the O_2 cost of cycling in humans (26). A significant study that highlighted the role of body mass in GE and DE was published by Berry *et al*. (23), who showed that GE and net efficiency, but not DE, during moderate intensity cycling examined in a heterogenous group of subjects, were negatively correlated with body mass. The authors (23), as others before (24, 27) considered that a greater body mass would decrease the GE by increasing the work of moving the legs during cycling. That portion of the mechanical work performed during exercise, which does not lead to generation of external power output or to changes of the centre of mass of the body, is called 'internal work' (28), but as revealed by Ettema and Loras (29), the precise measurement of the 'internal work' during cycling is indeed very difficult. It should be noticed that in recent years the issue of an impact of body mass or leg muscle mass on GE during cycling received, surprisingly, very little attention (4).

In the present study we hypothesized that a greater body mass would not only affect the cost of unloaded cycling by a greater cost of moving the heavier limbs during cycling, as proposed by Berry *et al*. (23), but would also increase resting metabolic rate (30-32), which would then independently increase the $V'O_2$ related to unloaded cycling and decrease GE. In other words, we postulate that the primary impact of body mass on GE is related to resting $V'O_2$ (higher body mass leading to higher resting $V'O_2$, leading to poorer GE), whereas the effects of body mass on DE (in the calculation of which resting $V'O_2$ is not considered) would not be significant.

MATERIALS AND METHODS

Participants and ethical approval

We studied 17 young, healthy male volunteers: age 23 ±3 years (min–max: 20–28 years); body mass 72.5 ±7.9 kg (min–max: 59.0–87.0 kg), body height 1.78 ±0.04 m (min–max: 1.71–1.86 m), body mass index (BMI) 22.6 ±2.0 $kg \cdot m^{-2}$ (min–max: 19.5–26.8 $kg \cdot m^{-2}$), $V'O_{2max}$ 3.668 ±0.404 $L \cdot min^{-1}$ (min–max: 2.526–4.252 $L \cdot min^{-1}$), PO_{max} at $V'O_{2max}$ 288 ±27 W (min–max: 240–330 W). The BMI was calculated as body mass divided by body height squared. All participants were non-smokers and were not taking medications or supplements. They were on standard mixed diet. The subjects were recreationally active. No one was specifically trained with cycling.

The experimental protocol was approved by the Ethics Committee of The Regional Medical Chamber in Cracow (no 48/KBL/OIL/2009) and was performed according to guidelines of the Declaration of Helsinki. All participants were fully informed of experimental procedures and written informed consent was obtained.

Exercise protocols

During the first visit to the laboratory the subjects were familiarized with all procedures and their body mass and height were determined. During the subsequent visit all subjects performed a maximal incremental test on an electromagnetically braked cycle ergometer (Ergoline GmbH, Bitz, Germany) to determine maximal oxygen uptake ($V'O_{2max}$) and the PO at $V'O_{2max}$. The exercise protocol started with 6 min of rest (subjects sitting on the cycle ergometer), followed by an increase of power output (PO) by 30 W every 3 min. The maximal incremental test was stopped when the subjects could no longer continue cycling at the required pedalling rate of 60 $rev \cdot min^{-1}$, or were unable to maintain the planned power output.

At least 7 days later the subjects performed a submaximal incremental test (series of 6 minutes bouts of increasing intensity) on the same cycle ergometer; pulmonary gas exchange variables (see below) including oxygen uptake ($V'O_2$) were determined. The test started with 6 min of rest (subjects sitting on the cycle ergometer), followed by a gradual increase of PO by 30 W every 6 min. This test was continued until the subjects reached about 90% of $V'O_{2max}$, established individually during the maximal incremental test. The pedalling rate during both tests was maintained at about 60 $rev \cdot min^{-1}$, which was imposed by a metronome. The participants did not perform any intense physical activity on the day before the tests. They consumed a light meal at least two hours before the test. The $V'O_2$ measured and the power outputs generated on the ergometer were used to calculate energy expenditure (EE), gross efficiency (GE) and delta efficiency (DE) during sub-lactate threshold (LT) PO's as described below, see equations 1 and 2.

Heart rate

The heart rate (HR) was monitored continuously by the ECG tracing (SMS 181, Hellige GmbH, Freiburg, Germany) during both incremental exercise tests.

Gas exchange variables

Oxygen uptake ($V'O_2$), carbon dioxide excretion ($V'CO_2$), pulmonary ventilation (V'E), and other variables were measured continuously breath by breath using the Oxycon Champion (Mijnhardt BV, Bunnik, Netherlands). The detailed description of the calibration of the metabolic cart is available in Zoladz *et al*. (16). The measurements started during the 6 minutes resting period before the onset of the exercise (subjects sitting on the cycle ergometer), and was continued until termination of the exercise protocols. The resting $V'O_2$ data are presented as mean ±S.D. of the 6 minutes measurements. The values of the gas exchange variables reached at the highest power output during the maximal incremental test protocols are presented as the mean values obtained during the last minute of this protocol, *i.e.* at exhaustion. The power output at $V'O_{2max}$ was defined as the power output at which $V'O_{2max}$ was reached during the maximal incremental test protocol. $V'O_{2max}$ was considered the highest $V'O_2$ oxygen uptake which did not further increase despite increasing PO. Values of gas exchange variables corresponding to the lactate threshold (LT) were determined.

Lactate threshold

Blood samples were collected at rest and at the end (last 10 s) of each step of the incremental protocols in order to determine the lactate threshold (LT). The detailed description of blood sampling and its preparation for the lactate measurements are available in Zoladz *et al*. (33). Lactate concentration was determined using the analyzer Vitros 250 Dry Chemistry System, Kodak, (Rochester, NY, USA). The lactate threshold was defined as the highest power output above which plasma lactate concentration ($[La^-]_{pl}$) showed a progressive increase ≥0.5 ($mmol \cdot L^{-1}$), according to (16, 34).

Calculation of cycling efficiency

Muscle mechanical efficiency during cycling was calculated both as gross efficiency (GE) and delta efficiency (DE) (2, 4). GE was calculated as power output divided by energy expenditure (EE), according to the following equations (9).

[1]:

$$\mathrm{GE} = \frac{Power\ Output}{EE} \cdot 100\%$$

[2]:

$$\mathrm{EE} = \frac{\dot{V}O_2\ (\mathrm{mL \cdot min^{-1}}) \cdot \left(\left(\left(\frac{\mathrm{RER} - 0.71}{0.29} \right) \cdot 21.4\ \mathrm{J \cdot (mL\ O_2)^{-1}} \right) + \left(\left(\frac{1.0 - \mathrm{RER}}{0.29} \right) \cdot 19.4\ \mathrm{J \cdot (mL\ O_2)^{-1}} \right) \right)}{60\ \mathrm{s}}$$

DE was calculated as the inverse slope of the linear relationship of EE vs. PO, as previously described by Gaesser and Brooks (2). The data of the respiratory exchange ratio (RER), $V'O_2$ and PO for this calculations were collected during the incremental sub-maximal exercise protocol. The efficiency (DE and GE) was determined only for the range of power outputs (30–120 W) which did not exceed LT; for these PO the RER was less than 1. The DE and the GE were calculated based on the gas exchange variables ($V'O_2$ and RER, see equations 1 and 2) obtained between the 4^{th}–6^{th} min of each power output (30, 60, 90 and 120 W) - for each individual. The DE was presented for each person as a single value for the studied range of power outputs (30–120 W). The individual DE and GE data were used for an appropriate correlations. For general overview the computed individual DE and GE values were also presented as mean ±SD (for 17 individuals).

Statistical analysis

The data are presented as the means ±standard deviations (SD). Correlations between variables were expressed using the Pearson's correlation coefficient. The significance level was set at 0.05. All linear regression models were estimated with the standard least-squares method. Approximate standard deviations of the reciprocals of the estimated slopes were computed by means of local linearization (the delta-method). Statistical significance of differences for paired samples was tested using non-parametric Wilcoxon-signed-rank test. Statistical analyses were performed by using the statistical package STATISTICA v. 13.3 (StatSoft, Warsaw, Poland).

RESULTS

Cardio-respiratory variables

The mean values of cardio-respiratory variables, obtained at rest and at maximal power output during the incremental maximal exercise protocol, as well as at rest and at LT during the incremental submaximal exercise protocol are presented in *Table 1*.

$V'O_2$ versus power output

The relationships between PO and absolute $V'O_2$ ($L \cdot min^{-1}$) (*Fig. 1A*) and PO vs. relative $V'O_2$ ($mL \cdot kg^{-1} \cdot min^{-1}$) (*Fig. 1B*) during the incremental submaximal exercise test are presented,

Table 1. Values (mean ±SD) of the cardio-respiratory variables measured at rest and at the maximal power output (PO_{max}) during the incremental maximal exercise protocol - until exhaustion, as well at rest and at the lactate threshold (LT) of the submaximal incremental exercise protocol (n=17).

Variables	**Maximal incremental test**		**Sub-maximal incremental test**	
	at rest	**at PO_{max}**	**at rest**	**at PO_{LT}**
$V'O_2$ ($L \cdot min^{-1}$)	0.33 ±0.06	3.67 ±0.40	0.29 ±0.07	1.93 ±0.26
$\%V'O_{2max}$	9 ±1	100	7 ±3	53 ±5
$V'O_2$ ($mL \cdot min^{-1}\ kg^{-1}$)	4.58 ±0.72	50.87 ±5.94	3.98 ±0.80	26.76 ±3.84
$V'CO_2$ ($L \cdot min^{-1}$)	0.31 ±0.06	4.08 ±0.41	0.26 ±0.07	1.83 ±22
V'_E ($L \cdot min^{-1}$)	12.7 ±2.3	119.7 ±19.0	11.2 ±2.5	49.7 ±6.4
RER ($mL \cdot min^{-1}$)	0.92 ±0.08	1.09 ±0.06	0.89 ±0.07	0.95 ±0.04
$[La^-]_{pl}$ ($mmol\ L^{-1}$)	1.4 ±0.2	9.3 ±1.7	1.4 ±0.5	1.8 ±0.5
Heart rate (bpm)	75 ±13	190 ±7	76 ±15	134 ±12
% HR_{max}	40 ±7	100	40 ±7	70 ±6

Abbreviations: $V'O_2$, minute oxygen uptake; $V'CO_2$, minute carbon dioxide release; V'_E, minute pulmonary ventilation; RER, respiratory exchange ratio; $[La^-]_{pl}$, plasma lactate concentration; HR, heart rate, PO_{max}, maximal power output; PO_{LT}, power output corresponding to lactate threshold (LT). The values of the all studied variables at the PO_{max} and at the PO_{LT} were significantly higher than at rest - before the subsequent exercise test (maximal incremental and sub-maximal incremental, respectively), (p<0.01; Wilcoxon-signed-rank test).

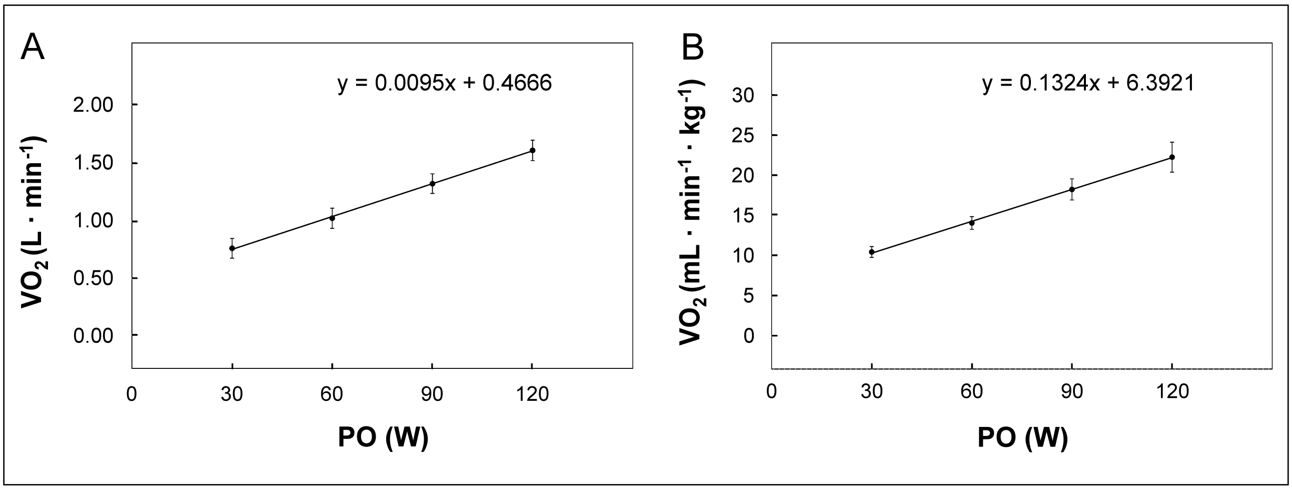

Fig. 1. Oxygen uptake ($V'O_2$) obtained during the sub-maximal incremental test, (expressed in $L \cdot min^{-1}$), determined as a function of PO (moderate intensity cycling) (panel A). Oxygen uptake ($V'O_2$) (expressed in $mL \cdot min^{-1}\ kg^{-1}$) determined as a function of PO (moderate intensity cycling), (panel B). The equations of the linear relationship between the $V'O_2$ and power outputs as presented in *Fig. 1A* and *1B* are based on the mean values of the $V'O_2$ of the studied group of subjects (n=17) reached at the four consecutive power outputs (30, 60, 90 and 120 W).

for PO<LT. $V'O_2$ values ranged between 28% and 53% of $V'O_{2max}$. For both variables on the y axes a linear relationship with PO was observed. The calculated DE was 29.8%.

The individual values (for all subjects, n=17) of the $V'O_2$ at rest, the slope and the intercept extracted from the equations of the linear regressions of $V'O_2$ vs. PO (30–120 W) obtained during submaximal test are presented in *Table 2*.

Delta efficiency

Table 3 shows the individual equations of the linear relationship between energy expenditure (EE, expressed in watts) and PO during cycling (incremental submaximal test) in the range from 30 W to 120 W, along with the corresponding delta efficiencies (DE) calculated from the inverse slope of the linear function (2). The mean value of DE was 29.8 ±1.9%.

Gross efficiency

GE expressed as (mean ±SD) for the power outputs of 30 W, 60 W, 90 W and 120 W, was 11.6 ±1.4%, 17.0 ±1.4%, 19.6 ±1.2%, 21.4 ±1.1%, respectively.

Body mass and $V'O_2$ at rest and intercepts and slopes of the $V'O_2$ (power output) relationships

Body mass ranged from 59 to 87 kg, and $V'O_2$ at rest ranged 144 to 415 $mLO_2 \cdot min^{-1}$. There was a significant positive correlation between body mass and $V'O_2$ at rest ($V'O_{2\ rest}$) (r=0.62, p<0.01) (*Fig. 2A*). The body mass was positively correlated with intercept of the $V'O_2$ vs. PO relationship determined for the range of PO 30–120 W (r=0.82, p<0.001), (*Fig. 2B*), the body mass was positively correlated with intercept of the $V'O_2$(PO) relationship (30–120 W) reduced by VO_2 at rest (r=0.55, p<0.05), (*Fig. 2C*), whereas there was no correlation between the body mass and slope of the $V'O_2$(PO) relationship (*Fig. 2D*).

The GE was negatively correlated with the intercept of the EE vs. PO relationship, calculated at PO of 30 W, 60 W, 90 W and 120 W (*Fig. 3A-3D*). In other words, the unloaded cycling $V'O_2$ was negatively and linearly related to GE, and a higher unloaded cycling $V'O_2$ was associated with a lower GE.

Body mass and delta efficiencies

No significant relationships were observed between body mass and DE or between $V'O_{2rest}$ and DE. The body mass (kg) vs. DE (%) relationship was as follows: y=0.243+0.0008x; *r*(Pearson)=0.27, p=0.297 (*Fig. 2E*) and the $V'O_{2rest}$ ($mL \cdot min^{-1}$) vs. DE (%) correlation was: y=0.2876+3.4364E-5x; *r*(Pearson)=0.11, p=0.670 (*Fig. 2F*).

Body mass and gross efficiency

As presented in *Fig. 4*, body mass was inversely correlated with GE. The relationship was present at all power outputs (30, 60, 90 and 120 W), (*Fig. 4A-4D*). Namely, a higher GE was associated with a lower body mass.

$V'O_2$ at rest and gross efficiency

Fig. 5A-5D shows the significant negative correlations between $V'O_2$ at rest and the GE, at all studied PO's (30, 60, 90 and 120 W). In other words, $V'O_2$ at rest was negatively and linearly related to GE, and a higher $V'O_2$ at rest was associated with a lower GE.

Gross efficiency and $V'O_{2max}$

Significant negative correlations were found between GE (at all four PO's) and $V'O_{2max}$ when expressed in absolute values ($L \cdot min^{-1}$), (*Fig. 6A-6D*). Namely, greater GE at all PO's were obtained by the subjects with lower $V'O_{2max}$.

When $V'O_{2max}$ was expressed in relative values ($mL \cdot min^{-1} \cdot kg^{-1}$), there was no significant correlation between $V'O_{2max}$ and GE calculated for 30 W; 60 W; 90 W and 120 W (n=17). There was also no significant correlation between $V'O_{2max}$, expressed in absolute and relative values, and DE calculated for the four exercise intensities 30–120 W (n=17).

Gross efficiency and maximal power output$_{max}$

Significant negative correlations were found between GE (at all PO's) and PO_{max} (*Fig. 7A-7D*).

Table 2. The individual data of the oxygen uptake ($V'O_2$) at rest and the slopes and the intercepts from the equations of linear regression of oxygen uptake ($V'O_2$) vs. power output (PO) in the range from 30 W up to 120 W, obtained during the sub-maximal incremental test. The coefficient of determination (R^2) was in all cases amounted to at least 0.99.

Subjects	**$V'O_2$ at rest** ($mL \cdot min^{-1}$)	**Slope** ($mLO_2 \cdot min^{-1}$ W^{-1})	**Intercept** ($mLO_2 \cdot min^{-1}$)
A1	289	9.51	431
A2	324	10.49	438
A3	144	9.29	306
A4	260	10.48	450
A5	415	9.46	576
A6	252	10.22	384
A7	392	9.12	570
A8	287	9.77	404
A9	404	8.64	549
A10	317	9.79	425
A11	276	10.16	460
A12	249	8.99	476
A13	239	9.69	399
A14	269	8.19	533
A15	196	9.70	310
A16	301	8.19	604
A17	318	9.45	621
Mean ±SD	290.1 ±70.4	9.48 ±0.70	466.6 ±95.7

Table 3. The individual equations of linear regression of energy expenditure (EE) vs. power output (PO) in the range from 30 W to 120 W, obtained during the incremental submaximal exercise protocol; where: y=EE (W) and x=PO (W). Delta efficiency (DE) was calculated as the reciprocal of the estimated slope in the EE (PO) relationship and the corresponding SD as the standard deviation of the estimated slope, divided by its square (the delta-method). The coefficient of determination R^2 was in all cases greater than 0.99.

Subject	**Equations of linear regression**	**DE**	**SD**
A1	y = 3.42x + 140	29.3%	1.9%
A2	y = 3.72x + 148	26.9%	1.9%
A3	y = 3.28x + 101	30.5%	1.4%
A4	y = 3.61x + 149	27.7%	2.7%
A5	y = 3.42x + 196	29.2%	1.4%
A6	y = 3.64x + 132	27.5%	2.0%
A7	y = 3.28x + 187	30.5%	2.9%
A8	y = 3.48x + 141	28.7%	1.5%
A9	y = 3.13x + 192	31.9%	2.7%
A10	y = 3.44x + 149	29.1%	1.6%
A11	y = 3.63x + 148	27.5%	0.9%
A12	y = 3.20x + 160	31.3%	3.6%
A13	y = 3.39x + 130	29.5%	0.4%
A14	y = 2.93x + 181	34.2%	2.3%
A15	y = 3.52x + 105	28.4%	2.8%
A16	y = 2.92x + 212	34.2%	1.0%
A17	y = 3.27x + 204	30.5%	1.4%

DISCUSSION

In the present study we have examined the impact of body mass on muscle efficiency during moderate intensity cycling in humans (young healthy untrained males), by taking in consideration gross efficiency (GE) and delta efficiency (DE) in a sub-LT range of power outputs. As expected, a linear relationship between $V'O_2$ and PO was observed. GE increased with PO, and

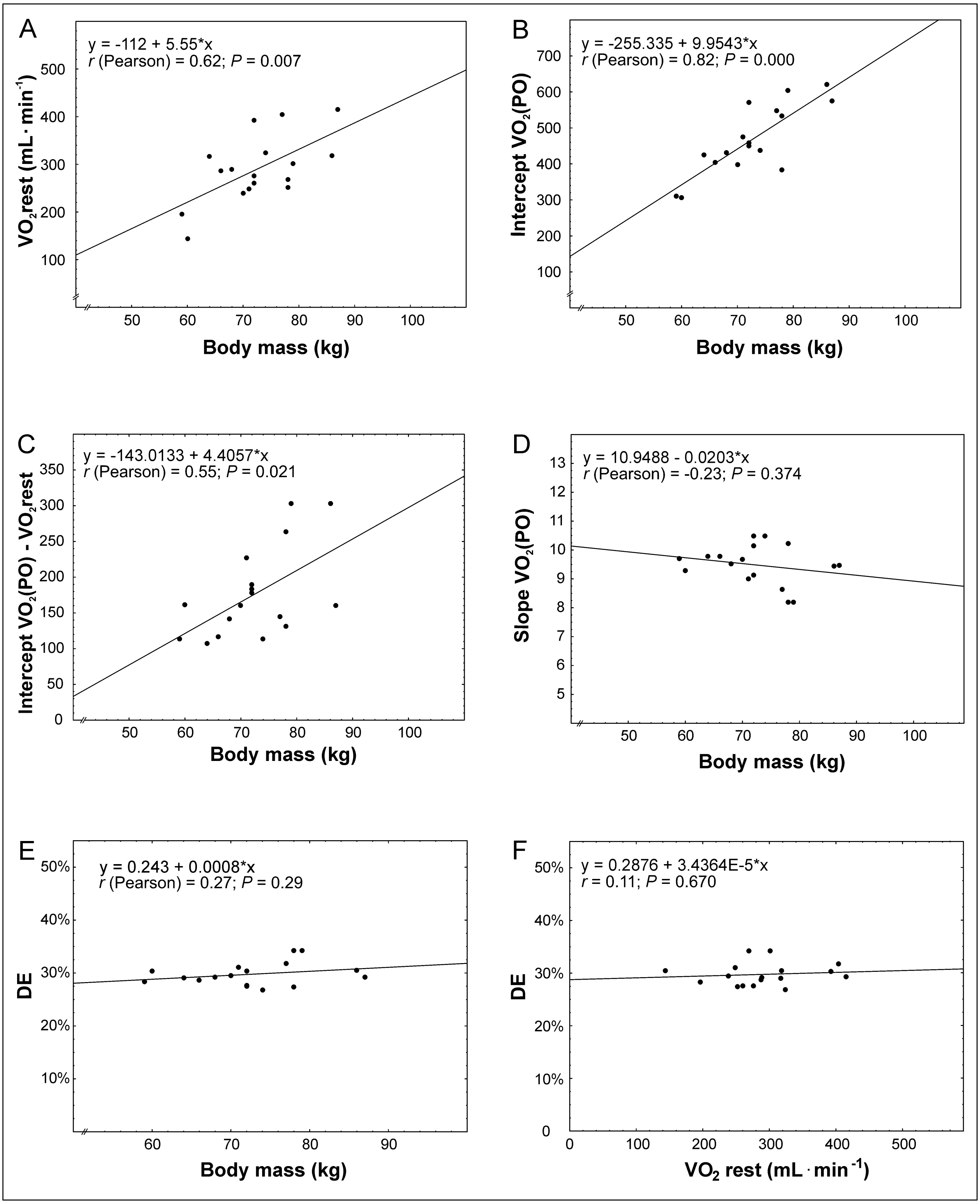

Fig. 2. The dependence between: the V'O_2 at rest and the body mass (panel A), the intercept of the V'O_2(PO) relationship and the body mass (panel B); the intercept of the V'O_2(PO) relationship (30–120 W) reduced by the V'O_2 at rest (*'*net intercept') and the body mass (panel C); slope of the V'O_2(PO) relationship and the body mass (panel D); the DE and the body mass (panel E); as well as the DE and the V'O_2 at rest (panel F).

its value at the highest PO (120 W) was 21.4 ±1.1%, close to that reported previously by others (2, 4). Also the lower GE at lower PO was described previously (2, 4), and it can be explained by a greater contribution by resting V'O_2 at low PO. Furthermore, the mean DE calculated in the present study (29.8 ±1.9%) was very close to that published previously by others (2, 4, 10).

The main and original finding of our study was that body mass related V'O_2 at rest significantly affects GE during

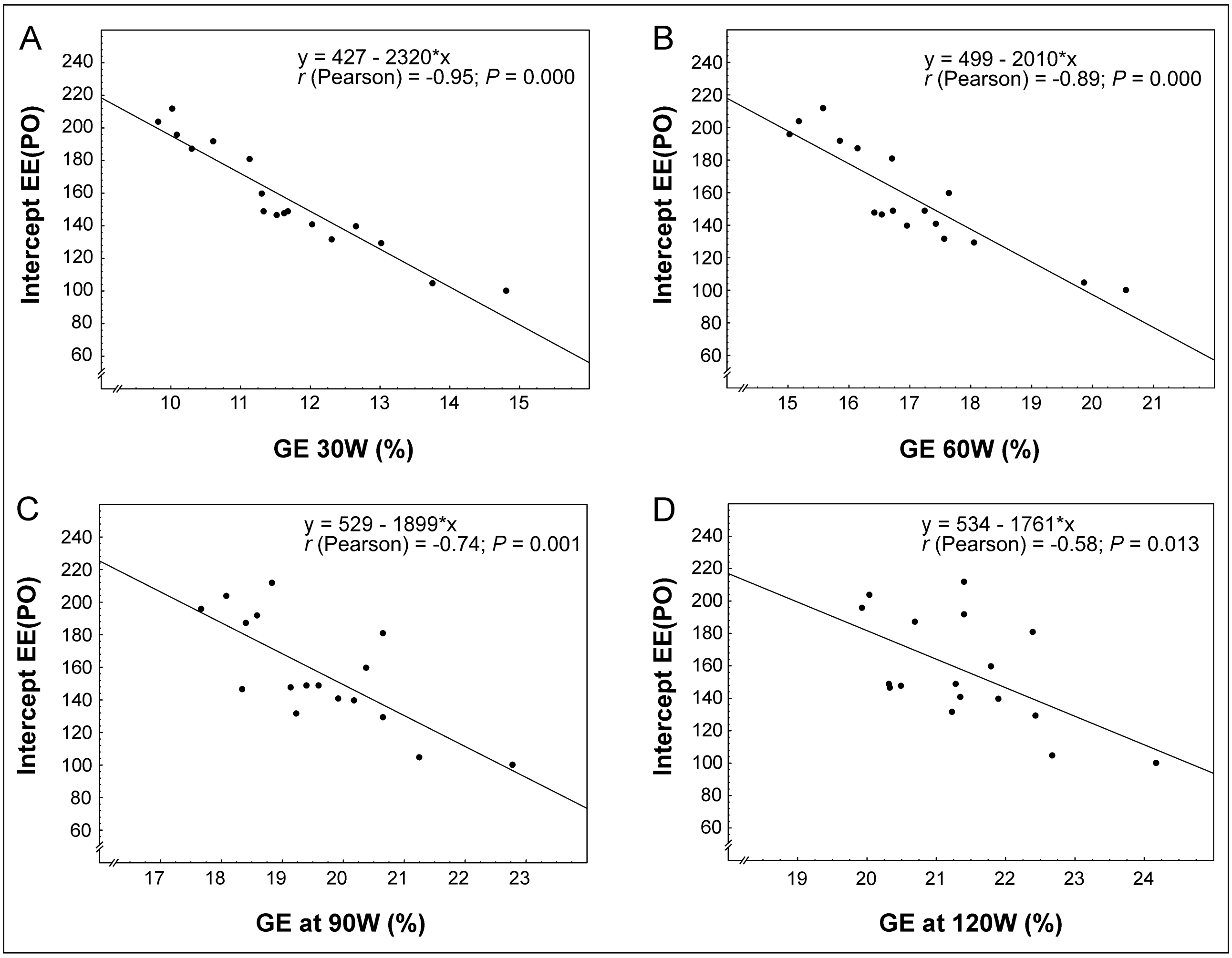

Fig. 3. Dependence of the intercept of the EE(PO) relationship on the gross efficiency (GE). The GE was calculated for four consecutive exercise intensities: (A) 30 W; (B) 60 W; (C) 90 W; (D) 120 W (n=17).

moderate intensity cycling. Namely, the subjects' body mass (range 59–87 kg) was positively correlated with V'O_2 at rest (expressed in absolute values) (p<0.01) (*Fig. 2A*) and with the intercept of the V'O_2(PO) relationship (p<0.01) (*Fig. 2B*), whereas there was no significant correlation between body mass and the slopes of V'O_2(PO) or EE(PO) relationships (*Fig. 2D*). Since, the intercept of the V'O_2(PO) relationship can be considered as an approximation of the energy expenditure of the unloading cycling (2, 28), our results show that the body mass influences the energy cost of unloaded cycling (*Fig. 2B*), which is in the agreement with the results by Berry *et al.* (23). Interestingly, we have also demonstrated a positive correlation between the intercept of the V'O_2(PO) relationship (30–120 W) reduced by the V'O_2 at rest ('net intercept') with the body mass (*Fig. 2C*). This strengths the above presented notion concerning the negative impact of the body mass on the oxygen cost of unloaded cycling, as postulated before by Berry *et al.* (23) and others (24, 27). Furthermore, our results demonstrate that in heavier subjects V'O_2(PO) and EE(PO) linear relationships are shifted upwards, without any systematic change of their slopes. In other words, heavier subjects (at least young healthy males and in the range of body mass taken in consideration by our study), have a higher resting V'O_2 (*Fig. 2A*) and a higher EE during unloaded cycling (*Fig. 2B*), whereas DE (as evaluated by the reciprocal slope of V'O_2(PO) or of EE(PO)) is not modified (*Fig. 2E*). The results of our study are in agreement with the study by Wasserman and Whipp (25) reporting a close positive correlation between the V'O_2 cost of unloaded cycling with subjects body mass (*Fig. 10* therein) resulting in an up-ward shift of the V'O_2 - power output relationship in the obese *vs.* normal subjects during moderate intensity cycling (see *Fig. 2.7* in (35)). It is worth noting that Wasserman *et al.* (35), suggested that this effect is a consequence an additional energy cost of moving the heavier lower extremities. Our study however, for the first time shows that this up-ward shift of the V'O_2(PO) in the heavier people is caused by their greater V'O_2 at rest when compared to the people with a lower body mass. This is a novel explanation of this phenomenon. Therefore, our study showed that the V'O_2 at rest related to the body mass affects the GE. This is a new finding no published before. Of course greater V'O_2 at rest will also contribute to greater O_2 cost of unloaded cycling, as presented in the present study, but the primary cause of the poorer GE in more heavier people originates from their higher basal metabolic rate as stated in the present paper.

Body mass and the delta efficiency

Our results are in agreement with previous studies concerning the impact of body mass on DE (23), confirming that body mass in a physiological range (~60–90 kg) in young healthy men has no impact on the muscle efficiency evaluated according to the DE concept. No inferences can of course be made on females, underweight or obese subjects, older people, or athletes specifically trained with cycling. Further studies could be

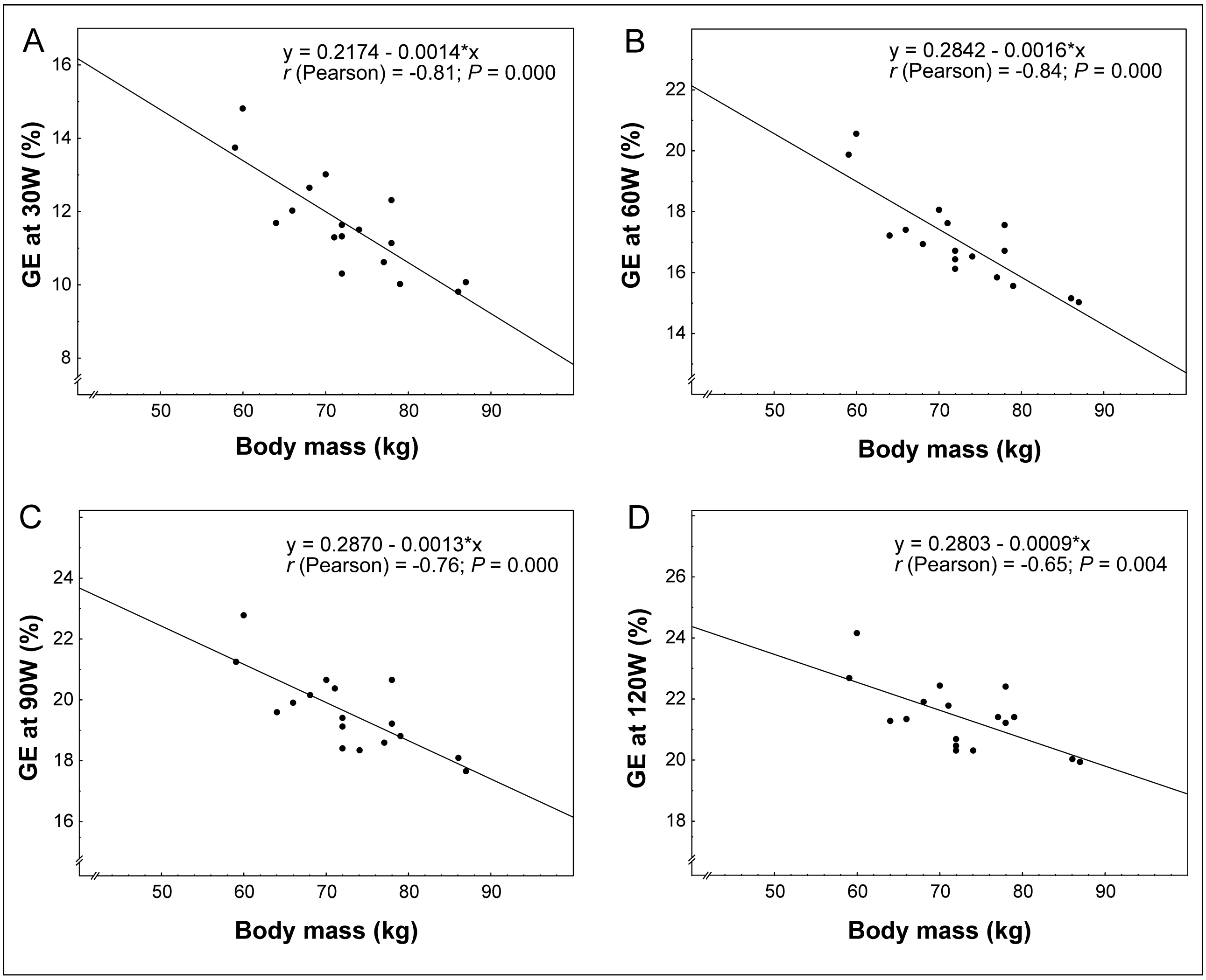

Fig. 4. Dependence of the gross efficiency (GE) on the body mass. The GE was calculated for four consecutive exercise intensities: (A) 30 W; (B) 60 W; (C) 90 W; (D) 120 W (n=17).

conducted on these populations. Interestingly, no relationship was found between DE and $V'O_{2max}$, nor with power generation capacity at $V'O_{2max}$. In other words, at least for the young, healthy and untrained men involved in this study, DE determined at sub-LT exercise was not related to the $V'O_{2max}$ and PO_{max} magnitude.

Body mass, resting $V'O_2$ and the gross efficiency

As one could expect, in the present study we found positive correlation between body mass and $V'O_2$ at rest (*Fig. 2A*). Furthermore, we have found a significant positive correlation between body mass and the intercept of $V'O_2$(PO) (*Fig. 2B*). This observation demonstrates that a higher body mass is associated with a greater $V'O_2$ of unloaded cycling, as expressed by greater values of the intercept of $V'O_2$(PO). Since the metabolic rate of unloaded cycling is the sum of the resting metabolic rate and the metabolic rate required for performing the 'internal work' (29), then the observed shift of the $V'O_2$(PO) in the individuals with higher body mass (*Fig. 2B*) would be caused not only by an increased 'internal work', as postulated previously (23, 24, 27), but also by an increased resting metabolic rate, attributable to a greater body mass (30-32). The elevated $V'O_2$ of unloaded cycling would lead to a lower GE during cycling at a given PO. In the present study we indeed observed a negative correlation between body mass and GE at sub-LT power outputs (*Fig. 4A-4D*). At a first glance our results appear to support the explanation offered by Berry *et al.* (23), that body mass influences GE *via* its impact on the energy expenditure during unloaded cycling, but the: (i) positive correlation between the body mass and $V'O_2$ at rest (*Fig. 2A*), (ii) the negative correlation between body mass and GE (*Fig. 4A-4D*); (iii) the negative correlations between $V'O_2$ at rest and GE (*Fig. 5A-5D*) show that the metabolic rate at rest play a significant role in determining the GE during cycling in humans. It is worth noting that the $V'O_2$ at rest in our study, determined in a sitting position, amounting to 290 ±70 mL $O_2 \cdot min^{-1}$, was almost identical to that reported previously by Reger *et al*. (38) (290 ±20 mL $O_2 \cdot min^{-1}$) and close to that reported by Francescato *et al*. (28), (320 mL $O_2 \cdot min^{-1}$).

In our opinion the above presented impact of the resting $V'O_2$, related to the body mass, might also play a role in the frequently reported training-induced increase of GE in humans. Namely, the training-induced decrease of body mass might lead to an increase of GE independently from a potential increase of the muscle efficiency *per se*, however a such mechanism, to our knowledge has not been considered so far in athletes (36, 37).

Gross efficiency, $V'O_{2max}$ and power output at $V'O_{2max}$

An interesting and surprising finding of this study was the negative correlation observed between GE and $V'O_{2max}$ (when

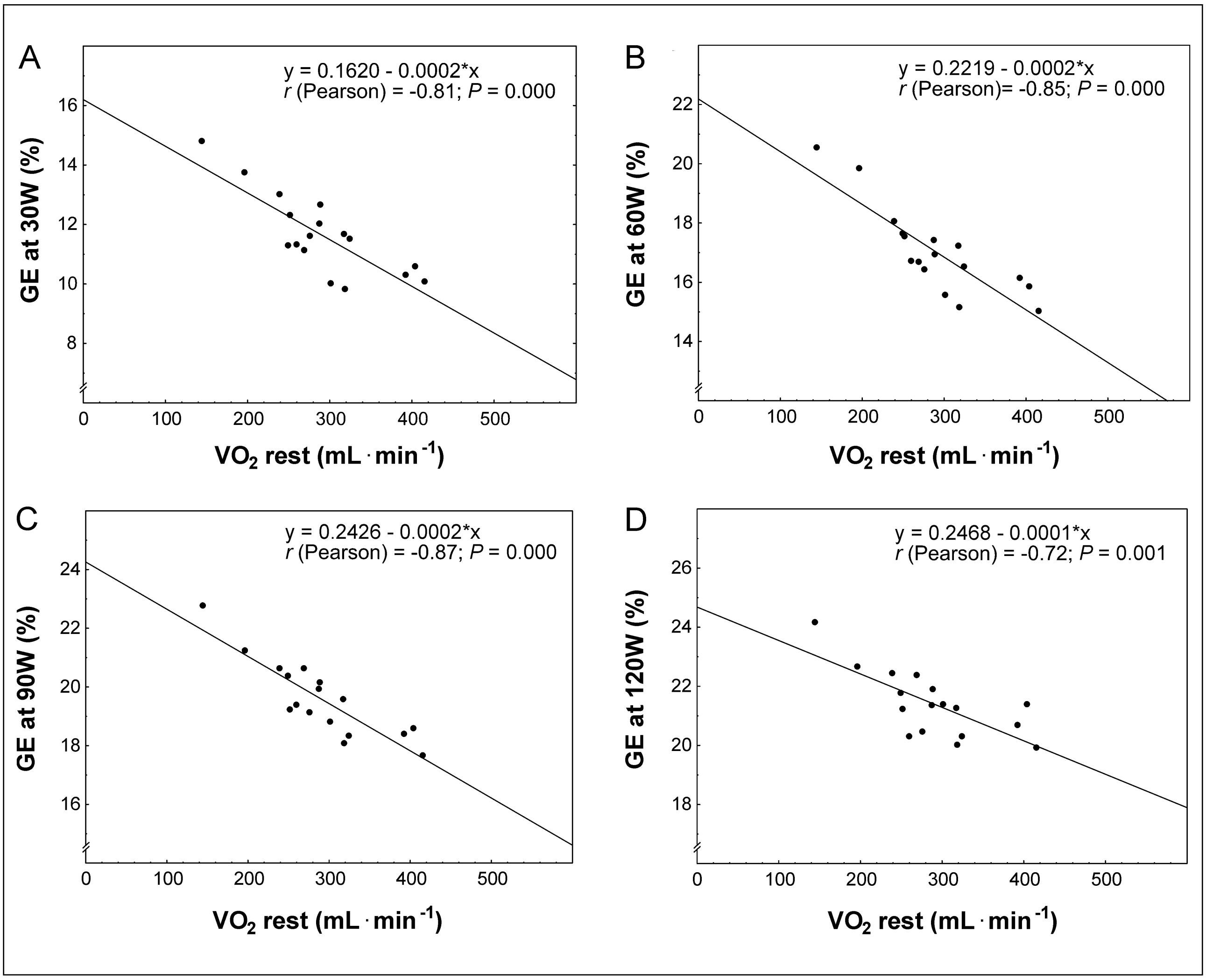

Fig. 5. Dependence of gross efficiency (GE) on the resting oxygen uptake ($V'O_{2rest}$). The GE was calculated for four consecutive exercise intensities: (A) 30 W; (B) 60 W; (C) 90 W; (D) 120 W (n=17).

expressed in absolute values) (*Fig. 6A-6D*) and the negative correlation between GE and power output at $V'O_{2max}$ (*Fig. 7A-7D*). As shown at all studied power outputs (30–120 W), lower GE were associated with higher absolute $V'O_{2max}$ (*Fig. 6A-6D*) and PO at $V'O_{2max}$ (*Fig. 7A-7D*). Interestingly, there was no correlation between GE and $V'O_{2max}$ when this variable was expressed in relative values (that is, when $V'O_{2max}$ was divided by body mass). Therefore, the GE determined at the sub LT exercise intensity appears to be a poor predictor of $V'O_{2max}$ expressed in relative units at least in the population tested in the present study. Our study indicates that the GE obtained during a sub LT exercise is determined by other factors than the $V'O_{2max}$ expressed in absolute units. Interestingly, body mass has an opposite effect on the GE and on the absolute $V'O_{2max}$. Namely, in young healthy untrained males a low body mass enhances GE but lowers the absolute $V'O_{2max}$ and the power generating capabilities near $V'O_{2max}$. It should be underlined that GE in our study by definition was examined during moderate intensity exercise, which intrinsically limits inferences on power outputs near $V'O_{2max}$. It should be underlined that the performance of a sub LT exercise in the moderate intensity domain, as in the present study, is accompanied by only very mild disturbances in muscle metabolite concentrations (7, 39). However, exceeding the LT or the critical power, results in a progressive increase of muscle metabolites such as ADP, P_i and H^+, associated with decreased muscle efficiency (7, 18, 22) and turns the $V'O_2$(PO) relationship from a linear (below the LT) to non-linear (when exercising above the LT - up to the $V'O_{2max}$) (7, 16, 40). This could be the reason why a high GE, when established below the LT, does not warrant a high power generating capabilities at $V'O_{2max}$. Furthermore, as shown in the present study, the low body mass (and most likely accompanied lower limb muscle mass), which is preferable for high GE, might actually limit the power generating capabilities at $V'O_{2max}$. This could be due to a greater absolute mechanical power requirements per unit of muscle mass at a given power output in slim persons when compared with heavier persons, when exercising at the $V'O_{2max}$, leading to earlier muscle fatigue.

In summary, our study demonstrated that $V'O_2$ at rest, correlated with body mass, is an important factor that affects GE during moderate intensity cycling in young healthy untrained men. Furthermore, we have shown that GE established at sub LT PO's is negatively correlated with $V'O_{2max}$ and with the PO at $V'O_{2max}$ (when expressed in absolute values), which illustrates that the GE is determined by different mechanisms than the $V'O_{2max}$ and the power generating capabilities at $V'O_{2max}$.

Perspective

Despite of the fact, that the assessment of the GE is a frequently conducted procedure when evaluating humans exercise

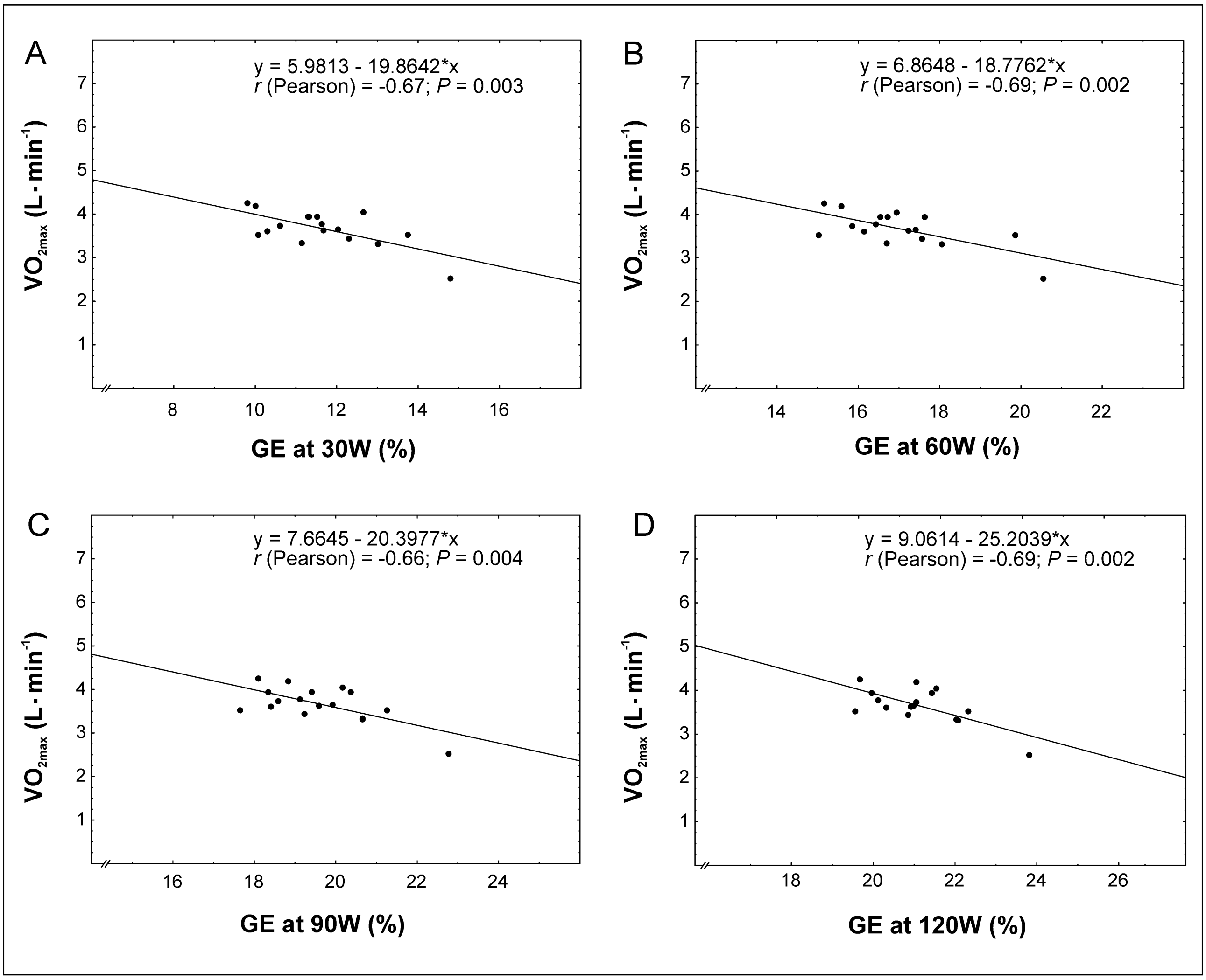

Fig. 6. The relationships between the maximal oxygen uptake ($V'O_{2max}$) expressed in absolute values with the gross efficiency (GE) calculated for the four consecutive exercise intensities: (A) 30 W; (B) 60 W; (C) 90 W; (D) 120 W (n=17).

capacity, however the influence of the body mass related resting $V'O_2$ on its level so far has been rather overlooked. The present study for the first time showed that the body mass related $V'O_2$ at rest negatively correlates with the GE in young healthy untrained men. Namely, an individuals with a greater body mass possess a poorer GE mainly due to a higher $V'O_2$ at rest. Therefore this factor should be considered when studying the humans muscles mechanical efficiency according to the GE concept. Furthermore, our study revealed that the GE and DE determined by definition at sub LT exercise intensities appear to be poor predictors of $V'O_{2max}$ expressed in relative units and reversly correlate with PO_{max}, at least in the population tested in the present study. Most likely, more significant inferences on maximal performance could derive from GE and DE data obtained during heavy-intensity exercise. In other words, one should be aware that the commonly used methods of determination of GE and DE based on $V'O_2$ measurements during exercise of sub LT intensities possess an intrinsic and significant limitations for prediction of maximal exercise capacity in humans. Therefore, our study shows that high body mass/overweight, regardless of its negative impact on human health (41-44), also contributes to poorer gross mechanical efficiency during exercise.

Abbreviations: ATP, adenosine triphosphate; ATP_{COST}, the ATP cost of force generation; ATP_{OX}, the efficiency of mitochondrial ATP synthesis; BMI, body mass index; BM, body mass; DE, delta efficiency; EE, energy efficiency; GE, gross efficiency; H^+, hydrogen ions; HR, heart rate; LT, lactate threshold; P_i, inorganic phosphate; PO, power output; PO_{max}, maximal power output reached at $V'O_{2max}$; ΔPO, power output difference; RER, respiratory exchange ratio; V'_E, minute pulmonary ventilation; $V'CO_2$, minute carbon dioxide release; $V'O_2$, minute oxygen uptake; $V'O_2$ at rest, minute oxygen uptake at rest; $V'O_{2max}$, minute maximal oxygen uptake; $\Delta V'O_2$, oxygen uptake difference.

Author's contribution: J.A.Z. designed the study; J.A.Z., M.G., and J.M. organized and performed experiments; J.A.Z., J.Z.B., M.G., Z.Sz., B.G., and J.M. analyzed and interpreted the data; J.A.Z., J.Z.B., and B.G. drafted and edited the manuscript. J.A.Z. is the guarantor of the study.

All authors approved of the final version for publication and agreed to be accountable for all aspects of the work. All persons designated as authors qualify for authorship, and all those who qualify for authorship are listed.

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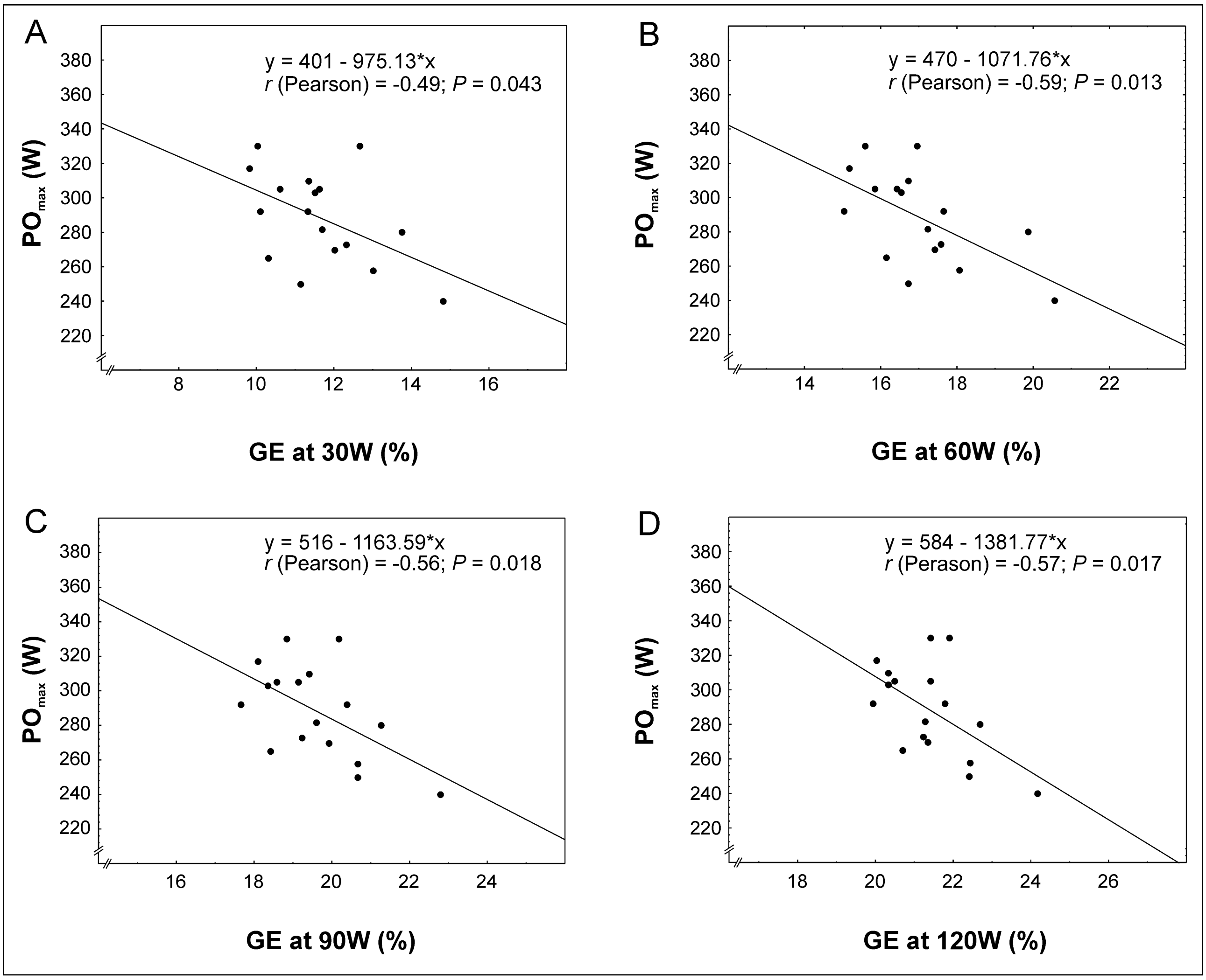

Fig. 7. The relationships between the power output reached at maximal oxygen uptake (PO at $V'O_{2max}$) with the gross efficiency (GE) calculated for the four consecutive exercise intensities: (A) 30 W; (B) 60 W; (C) 90 W; (D) 120 W (n=17).

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