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Pedalling rate affects endurance performance during high-intensity cycling

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Abstract The purpose of this study into high-intensity cycling was to: (1) test the hypothesis that endurance time is longest at a freely chosen pedalling rate (FCPR), compared to pedalling rates 25% lower (FCPR–25) and higher (FCPR + 25) than FCPR, and (2) investigate how physiological variables, such as muscle fibre type composition and power reserve, relate to endurance time. Twenty males underwent testing to determine their maximal oxygen uptake ($\dot{V}O_{2\max}$), power output corresponding to 90% of $\dot{V}O_{2\max}$ at 80 rpm ($\dot{W}90$), FCPR at $\dot{W}90$, percentage of slow twitch muscle fibres (% MHC I), maximal leg power, and endurance time at $\dot{W}90$ with FCPR–25, FCPR, and FCPR + 25. Power reserve was calculated as the difference between applied power output at a given pedalling rate and peak crank power at this same pedalling rate. $\dot{W}90$ was 325 (47) W. FCPR at $\dot{W}90$ was 78 (11) rpm, resulting in FCPR–25 being 59 (8) rpm and FCPR + 25 being 98 (13) rpm. Endurance time at $\dot{W}90_{\text{FCPR}+25}$ [441 (188) s] was significantly shorter than at $\dot{W}90_{\text{FCPR}}$ [589 (232) s] and $\dot{W}90_{\text{FCPR}-25}$ [547 (170) s]. Metabolic responses such as $\dot{V}O_2$ and blood lactate concentration were generally higher at $\dot{W}90_{\text{FCPR}+25}$ than at $\dot{W}90_{\text{FCPR}-25}$ and $\dot{W}90_{\text{FCPR}}$. Endurance time was negatively related to $\dot{V}O_{2\max}$, $\dot{W}90$ and % MHC I, while positively related to power reserve. In conclusion, at group level, endurance time was longer at FCPR and at a pedalling rate 25% lower compared to a pedalling rate 25% higher than FCPR. Further, inter-individual physiological variables were of significance for endurance time, % MHC I showing a negative and power reserve a positive relationship.

Keywords Freely chosen pedalling rate · Power reserve · Metabolic response · Muscle fibre type composition

Introduction

Freely chosen pedalling rate (FCPR) is higher than the energetically optimal pedalling rate at low to moderate exercise intensity. This implies that cycling at such sub-maximal exercise intensity at FCPR does not result in maximum gross efficiency (Hansen et al. 2002a; Marsh and Martin 1993; Vercruyssen et al. 2002). Furthermore, it was recently reported that FCPR during cycling increased with increasing exercise intensity (Hansen et al. 2002a), which is in agreement with the general finding that pedalling rate at minimum rating of perceived exertion increases with increasing exercise intensity (Hansen et al. 2002a; Löllgen et al. 1980). The interpretation of these combined findings could be that the effectiveness of human behaviour with regard to energy turnover during pedalling decreases with increasing exercise intensity. However, the energetically optimal pedalling rate increases with increasing exercise intensity (Hansen et al. 2002a; Seabury et al. 1977), reducing the difference between FCPR and the energetically optimal pedalling rate as the intensity of exercise increases, and making the two distinct pedalling rates merge at high exercise intensity (Brisswalter et al. 2000) (see also Fig. 1).

It seems plausible that high efficiency, corresponding to low energy turnover, would be crucial for maximum endurance performance during cycling at high exercise intensities. Based on this assumption, and in combination with the finding that FCPR and the energetically optimal pedalling rate merge at high exercise intensity, it may be expected that cycling at FCPR during high exercise intensity results in the best endurance performance, compared to cycling at lower or higher pedalling rates. An alternative hypothesis is that a mechanically

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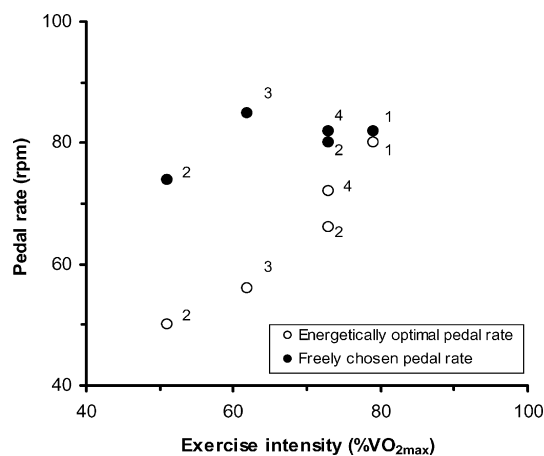


Fig. 1 Freely chosen pedalling rate and energetically optimal pedalling rate as a function of exercise intensity, given as the maximum percentage of oxygen uptake ($\dot{V}O_{2max}$). Data points represent group means. Numbers refer to references: 1, Brisswalter et al. (2000); 2, Hansen et al. (2002a); 3, Marsh and Martin (1993); 4, Vercruyssen et al. (2002). Only studies reporting both the freely chosen pedalling rate and the energetically optimal pedalling rate for the same group of subjects have been included

optimal pedalling rate, instead of the energetically optimal pedalling rate, is optimal for endurance performance. It has been established that maximum peak crank power is performed at relatively high pedalling rates, i.e. up to around 120 rpm (Beelen and Sargeant 1991; Hansen et al. 2002a; Hautier et al. 1996; McCartney et al. 1983; Sargeant 1987; Sargeant et al. 1981; Zoladz et al. 2000). This implies that power reserve, (the difference between applied power output at a given pedalling rate and peak crank power at this same pedalling rate) increases with increasing pedalling rate. Based on this, it may be expected that cycling at pedalling rates higher than FCPR, e.g. up to around 120 rpm, results in maximal endurance performance (Zoladz et al. 2000).

However, it is important to realise that some individual physiological characteristics interfere with both the energetically and the mechanically optimal pedalling rate. For example, it has been shown that maximal peak crank power is negatively related to the percentage of slow twitch muscle fibres (Hansen et al. 2002a). Accepting this result, and the above assumption that a high rather than a low power reserve results in a longer endurance performance, then a low compared to a high percentage of slow twitch muscle fibres should be superior for endurance performance. However, this is contrary to the general finding that slow twitch muscle fibres have a greater capacity for endurance than fast twitch fibres and, in terms of energy turnover, are more efficient during cycling (Coyle et al. 1992; Hansen et al. 2002a). Thus, there is still a crucial lack of knowledge regarding the combined interplay between the effect of mechanical work demands and metabolic responses, both of which are affected by changing pedalling rate, as well as subject characteristics on endurance performance during cycling at high exercise intensity.

The purpose of the present study was: (1) to test the hypothesis that endurance time during cycling at high exercise intensity is longest when cycling is performed at FCPR, compared to pedalling rates 25% lower and higher than FCPR, and (2) to investigate how physiological and mechanical variables, such as muscle fibre type composition and power reserve, relate to endurance time during cycling at high exercise intensity.

Methods

Subjects

Twenty healthy male subjects of age 26.3(3.5) years, height 1.78 (0.05) m, and body mass 73.5 (7.5) kg gave written informed consent to participate in the study, which was approved by the local ethical committee. The subjects were recruited to represent a large variation in muscle fibre type composition, in terms of MHC isoform distribution; the values are given as mean (SD) (range): 63 (17) (21–97)% MHC I, 33 (14) (4–65)% MHC IIa, and 3 (5) (0–5)% MHC IIx, as previously reported (Hansen et al. 2002a). The subjects performed cycling for transportation, recreation and/or sport, and, as with the majority of the Danish population, were all highly accustomed to cycling.

Exercise sessions

Three pre-sessions and three endurance sessions were conducted over a period of 10 weeks. The purpose of the pre-sessions was to determine: (1) maximal oxygen uptake ($\dot{V}O_{2max}$) and power output corresponding to 90% of $\dot{V}O_{2max}$ at 80 rpm ($\dot{W}90$); (2) maximal leg power, and (3) FCPR at $\dot{W}90$. The endurance sessions consisted of cycling at $\dot{W}90$ until exhaustion at three different pedalling rates corresponding to 25% lower than FCPR (FCPR–25), FCPR, and 25% higher than FCPR (FCPR+25).

Determination of $\dot{V}O_{2max}$ and $\dot{W}90$

The subjects performed cycling at 80 rpm on a Monark cycle ergometer (Monark AB, Varberg, Sweden), which was mounted with an SRM crank dynamometer (Schoberer Rad Messtechnik, Jülich, Germany) and Look pedals (Look Cycle, Nevers, France). A 5-min warm up at 100 W was followed by submaximal bouts at 150, 200 and 250 W, each of 5 min. Then, after 5 min of rest, the subjects performed a progressive test resulting in exhaustion within 4–7 min (Hansen et al. 2002a). During the last 2 min of each submaximal bout, and continuously from the 2nd min in the progressive test, expired air was collected in Douglas bags for analysis (Franch et al. 1998). Blood lactate concentration in blood samples taken from a fingertip 2 min after exhaustion was measured by a YSI 1500 Sport (YSI Incorporated, Yellow Springs, Ohio, USA). Analysis methods for the other sessions were the same as described here with regard to expired air and blood samples. Power output, pedalling rate, and heart rate were measured with the SRM crank dynamometer, which sampled data at 1 Hz. Subsequently, for each subject the relationship between power output and $\dot{V}O_2$ was plotted for determination of $\dot{W}90$, which was applied in the third pre-session and the endurance sessions.

Determination of maximal leg power and power reserve

The subjects performed cycling on a racing bicycle placed on a Woodway ELG 70 treadmill (Woodway GmbH, Weil am Rhein, Germany). The bicycle was mounted with an SRM crank dynamometer.

momenter and a custom-built handlebar, which was fastened to the treadmill handrail. The experimental setup allowed the subjects to pedal at maximal effort in an isokinetic mode without advancing the bicycle relative to the treadmill while the pedalling rate and crank torque were being recorded. Twelve isokinetic maximal cycling bouts at preset pedalling rates of 30–140 rpm in steps of 10 rpm were performed. Cycling speed and gear ratio were matched to attain the target pedalling rates. The cycling bouts lasted 5 s, were randomised, and separated by 3 min of rest. Four bouts were performed 1 h prior to each endurance session. For each subject, peak crank power was calculated from each bout as previously described (Hansen et al. 2002a). Maximum peak crank power was calculated from a second order equation fitted to the peak crank power data plotted against the pedalling rate. In addition, peak crank power for each of the three applied pedalling rates in the endurance sessions (FCPR–25, FCPR and FCPR + 25) was calculated by interpolation from the second order equation. Power reserve for each endurance session was calculated as: Power reserve = $[1.0 - (\dot{W}_{90}/\text{Peak crank power at the applied pedalling rate})] \cdot 100\%$.

In the context of the present text, a high power reserve corresponds to a low relative mechanical work demand and vice versa.

Determination of FCPR at \dot{W}_{90}

The subjects performed cycling on a 16-speed racing bicycle placed on a Woodway ELG 70 treadmill at $11.2 \text{ km} \cdot \text{h}^{-1}$. The bicycle was mounted with an SRM crank dynamometer. The combination of available gear ratios and the treadmill speed allowed subjects to choose pedalling rates in the range normally used by road cyclists during competition. The relatively low treadmill speed resulted in a crank inertial load comparable with that on a Monark ergometer cycle (Fregly et al. 2000; Hansen et al. 2002b). Power output was adjusted by changing the weight of a scale that was connected to a wire running over a pulley (placed behind the treadmill) and tied to the rear of the bicycle (Hansen et al. 2002a). After a 5-min warm up at 100 W, followed by a 5-min rest, subjects started cycling at \dot{W}_{90} for 5 min. During the first 3 min at \dot{W}_{90} subjects were allowed to change gear ratio in order to freely choose their pedalling rate. During the subsequent 2 min, FCPR was maintained while expired air was collected in Douglas bags and power output and pedalling rate was measured by the SRM crank dynamometer. The rating of perceived exertion (RPE) was stated at the end of the bout (Borg 1970). The FCPR at \dot{W}_{90} was calculated as the mean pedalling rate over the last 2 min and then the pedalling rates corresponding to FCPR–25 and FCPR + 25 were obtained.

Determination of endurance time

The subjects performed cycling on a Monark ergometer cycle mounted with an SRM crank dynamometer and Look pedals. Three endurance sessions were performed at \dot{W}_{90} with pedalling rates of FCPR–25 ($\dot{W}_{90_{\text{FCPR}-25}}$), FCPR ($\dot{W}_{90_{\text{FCPR}}}$) and FCPR + 25 ($\dot{W}_{90_{\text{FCPR}+25}}$), in a randomised order according to a balanced design. The sessions for each subject were held 1 week apart, always on the same day of the week and at the same time of day. The sessions started with a standardised warm up. Subjects performed 5 min of cycling at a power output corresponding to 40% of $\dot{V}O_{2\text{max}}$ (determined at 80 rpm) followed by 5 min of cycling at a power output corresponding to 70% of $\dot{V}O_{2\text{max}}$ (determined at 80 rpm). The pedalling rate used during warm up was the same as applied in the subsequent endurance session. Warm up was followed by 5 min of rest. After the rest period the subjects started cycling at \dot{W}_{90} until the pedalling rate in a 20-s period was more than 10 rpm below the preset pedalling rate or until the subjects stopped due to exhaustion. Subsequently, the endurance time was determined as the time until the pedalling rate in a 3-s period was more than 10% below the preset pedalling rate. During cycling, the pedalling rate was displayed in front of subjects by the SRM power

control. Subjects were informed that they needed to keep as close as possible to the preset pedalling rate, to maintain it for as long as they could and to not stop cycling before a sign was given by the experimenter. Power output, pedalling rate and heart rate were continuously monitored and stored by the SRM crank dynamometer. Expired air was collected in two Douglas bags from the 3rd to the 5th min and again from the 8th to the 10th min, etc., until exhaustion. Pulmonary gas exchange for a given period was calculated as a mean of the two Douglas bags. Pulmonary gas exchange at exhaustion corresponds to measurements from the last collected Douglas bags prior to exhaustion. Blood lactate concentration and RPE measurements were made after 5 min of cycling and repeated at exhaustion.

Statistics

Analysis of variance was performed using the Friedman test, and in case of significance, the test was followed by the Wilcoxon signed rank test. Simple and multiple regressions were performed. All analyses were performed using StatView 5.0 (SAS Institute Inc., N.C., USA). $P \leq 0.05$ was considered to be statistically significant. Data are presented as mean (SD), occasionally followed by (range).

Results

Power output and FCPR

The calculated \dot{W}_{90} was 325 (47) W and the power output attained during treadmill cycling for determination of FCPR was 327 (54) W, which was not significantly different from \dot{W}_{90} . Further, there were no significant differences in power output between the three endurance sessions, the power output as an overall mean being 315 (47) W. However, this power output was on average 3% lower than power output in the third pre-session where FCPR was determined. The FCPR at \dot{W}_{90} during treadmill cycling was 78 (11) (59–94) rpm. Consequently, FCPR–25 was 59 (8) (44–70) rpm and FCPR + 25 was 98 (13) (74–117) rpm.

Maximal leg power and power reserve

Maximal peak crank power was 1412 (299) W and occurred at 122 (18) rpm [for more details see (Hansen et al. 2002a)]. Peak crank power at FCPR–25, FCPR and FCPR + 25 was 1081 (195), 1237 (200) and 1328 (213) W, respectively. Power reserve at $\dot{W}_{90_{\text{FCPR}-25}}$, $\dot{W}_{90_{\text{FCPR}}}$ and $\dot{W}_{90_{\text{FCPR}+25}}$ was 70.3 (5.0), 73.8 (5.1) and 75.9 (4.5)%, respectively. Both peak crank power and power reserve increased significantly with pedalling rate.

Endurance time

Endurance time at $\dot{W}_{90_{\text{FCPR}-25}}$, $\dot{W}_{90_{\text{FCPR}}}$ and $\dot{W}_{90_{\text{FCPR}+25}}$ was 547 (292–1027) s, 589 (252–1119) s and 441 (196–912) s, respectively (Fig. 2). Thus, endurance time at $\dot{W}_{90_{\text{FCPR}+25}}$ was on average 25% shorter than at $\dot{W}_{90_{\text{FCPR}}}$, and on average 19% shorter than at $\dot{W}_{90_{\text{FCPR}-25}}$; these differences being significant. Endur-

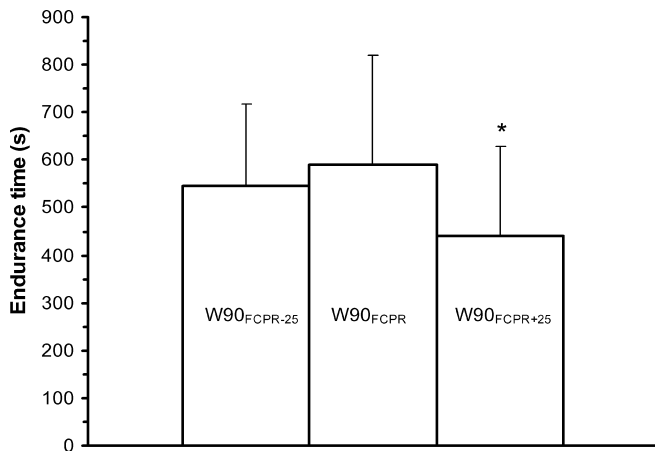


Fig. 2 Endurance time at the three endurance sessions: $\dot{W}90_{FCPR-25}$, $\dot{W}90_{FCPR}$ and $\dot{W}90_{FCPR+25}$, where $\dot{W}90$ is power output corresponding to 90% of $\dot{V}O_{2max}$ at 80 rpm, FCPR is the freely chosen pedalling rate, and FCPR-25 and FCPR+25 are pedalling rates 25% lower and higher than FCPR. Data are presented as mean (SD). * Significantly different from $\dot{W}90_{FCPR-25}$ and $\dot{W}90_{FCPR}$

ance time was not significantly different between $\dot{W}90_{FCPR-25}$ and $\dot{W}90_{FCPR}$.

Physiological responses

$\dot{V}O_{2max}$ was 4.42 (0.61) l·min⁻¹ while $\dot{V}O_2$ during treadmill cycling at $\dot{W}90$ in the third pre-session was 4.12 (0.57) l·min⁻¹. Regarding the endurance sessions, $\dot{V}O_2$ after 5 min at $\dot{W}90_{FCPR+25}$ was on average 5 and 7% higher than at $\dot{W}90_{FCPR}$ and $\dot{W}90_{FCPR-25}$, respectively (Table 1). In line with this, at exhaustion the general pattern was that $\dot{V}O_2$ was highest at $\dot{W}90_{FCPR+25}$ and lowest at $\dot{W}90_{FCPR-25}$. The maximal pulmonary ventilation (\dot{V}_E) during determination of $\dot{V}O_{2max}$ was 163 (38) l·min⁻¹. During treadmill cycling at $\dot{W}90$, \dot{V}_E was 132 (26) l·min⁻¹. Values on \dot{V}_E from the endurance sessions are presented in Table 1. The maximal RER during determination of $\dot{V}O_{2max}$ was 1.20 (0.05). During

treadmill cycling at $\dot{W}90$, RER was 1.10 (0.07). Values on RER from the endurance sessions are presented in Table 1. The maximal heart rate during determination of $\dot{V}O_{2max}$ was 190 (10) beats per min (bpm). Regarding the endurance sessions, heart rate after 5 min of cycling at $\dot{W}90_{FCPR+25}$ was on average 2 and 3% higher than at $\dot{W}90_{FCPR}$ and $\dot{W}90_{FCPR-25}$, respectively. There was no difference in heart rate at exhaustion between the three endurance sessions (Table 1). The maximal blood lactate concentration during determination of $\dot{V}O_{2max}$ was 12.2 (2.0) mmol·l⁻¹. Regarding the endurance sessions, blood lactate concentration after 5 min at $\dot{W}90_{FCPR+25}$ was on average 25 and 36% higher than at $\dot{W}90_{FCPR}$ and $\dot{W}90_{FCPR-25}$, respectively. Blood lactate concentration at exhaustion after $\dot{W}90_{FCPR+25}$ was on average 6 and 9% higher than at $\dot{W}90_{FCPR}$ and $\dot{W}90_{FCPR-25}$, respectively (Table 1). The RPE was 16.6 (1.5) after 5 min of treadmill cycling at $\dot{W}90$ in the third pre-session. This was not significantly different from the RPE after 5 min at $\dot{W}90_{FCPR}$ in the endurance session (Table 1). No significant differences were found in the RPE after 5 min and at exhaustion between the three endurance sessions (Table 1).

Endurance time relative to physiological and mechanical variables

Significant negative relationships were found between $\dot{V}O_{2max}$, expressed as ml·min⁻¹·kg⁻¹, and endurance time, with r -values between -0.47 and -0.64 being obtained for the different endurance sessions. The same tendency was found for $\dot{V}O_{2max}$, expressed as l·min⁻¹, with r -values of between -0.31 and -0.40, although these were not significant. Since $\dot{W}90$ was related to $\dot{V}O_{2max}$ (l·min⁻¹) ($r=0.96$), negative relationships were also expected, and seen, between $\dot{W}90$ and endurance time, with r -values of between -0.44 and -0.49 (Fig. 3). Further, since $\dot{V}O_{2max}$ (l·min⁻¹) and % MHC I were related ($r=0.57$), negative relationships were seen between % MHC I and endurance time (r -values of between -0.44 and -0.58) and, again, this had been

Table 1 Oxygen consumption ($\dot{V}O_2$), ventilation (\dot{V}_E), respiratory exchange ratio (RER), heart rate, blood lactate concentration (Lactate), and rate of perceived exertion (RPE) from the three endurance sessions with $\dot{W}90$ (power output corresponding to 90%

$\dot{V}O_{2max}$ at 80 rpm) at FCPR (the freely chosen pedalling rate) and at 25% above and below FCPR. Data represent measurements made after 5 min and at exhaustion and are presented as mean (SD)

	After 5 min			At exhaustion		
	W90 _{FCPR-25}	W90 _{FCPR}	W90 _{FCPR+25}	W90 _{FCPR-25}	W90 _{FCPR}	W90 _{FCPR+25}
$\dot{V}O_2$ (l·min ⁻¹)	4.02 (0.55)	4.09 (0.57) ^b	4.30 (0.54) ^a	4.20 (0.54) ^c	4.27 (0.54) ^{b,c}	4.36 (0.57) ^{a,c}
\dot{V}_E (l·min ⁻¹)	116 (25)	121 (27)	134 (31) ^a	142 (22) ^c	146 (31) ^c	146 (32) ^c
RER	1.05 (0.05)	1.06 (0.05)	1.08 (0.06)	1.06 (0.05)	1.05 (0.05)	1.07 (0.07)
Heart rate (bpm)	175 (8)	176 (11)	181 (8) ^a	184 (8) ^c	184 (9) ^c	186 (8) ^c
Lactate (mmol·l ⁻¹)	7.4 (2.1)	8.1 (2.1)	10.1 (2.5) ^a	10.9 (2.7) ^c	11.2 (2.7) ^c	11.9 (2.5) ^{a,c}
RPE	17.1 (1.4)	16.7 (1.2)	17.2 (1.8)	18.9 (0.9) ^c	19.1 (0.7) ^c	19.0 (1.2) ^c

^a Significantly different from W90_{FCPR} and W90_{FCPR-25}, $P \leq 0.05$

^b Significantly different from W90_{FCPR-25} and W90_{FCPR+25}, $P \leq 0.05$

^c Significantly different from values after 5 min in the same session, $P \leq 0.05$

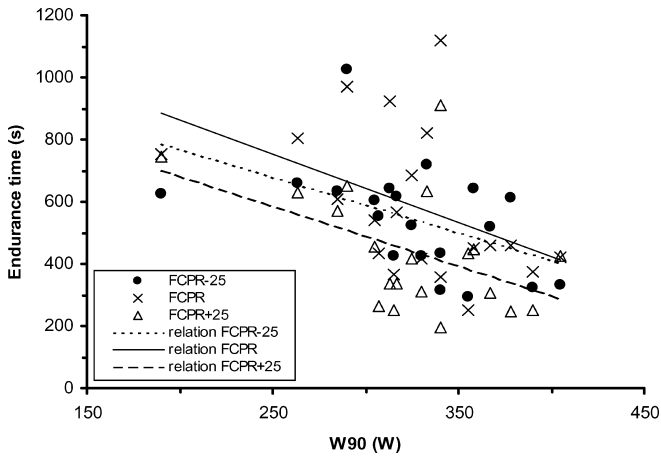


Fig. 3 Relationship between $\dot{W}90$ and endurance time at the three endurance sessions. All relations are significant and the equations of the regression lines are: Endurance time at $\dot{W}90_{FCPR-25} = -1.8(\dot{W}90) + 1129$, endurance time at $\dot{W}90_{FCPR} = -2.2(\dot{W}90) + 1305$ and endurance time at $\dot{W}90_{FCPR+25} = -1.9(\dot{W}90) + 1065$, with r -values of -0.49 ($P < 0.03$), -0.44 ($P = 0.05$), and -0.48 ($P = 0.03$), respectively

expected. Nevertheless, this appeared to be a puzzling finding. It is worth noting, however, that $\dot{V}O_{2max}$ and $\dot{W}90$ were unrelated to maximal peak crank power, which implied that those subjects with the highest $\dot{V}O_{2max}$ (and thus performing the highest $\dot{W}90$) worked at the relatively lowest power reserve. Interestingly, endurance time was positively related to power reserve, with r -values obtained of being between 0.56 and 0.85 (Fig. 4), while power reserve was negatively related to % MHC I, where the r -values were between -0.59 and -0.76 (Fig. 5). Performing multiple regression analyses with endurance time as the dependent variable and $\dot{V}O_{2max}$ ($l \cdot \text{min}^{-1}$), together with power reserve, as inde-

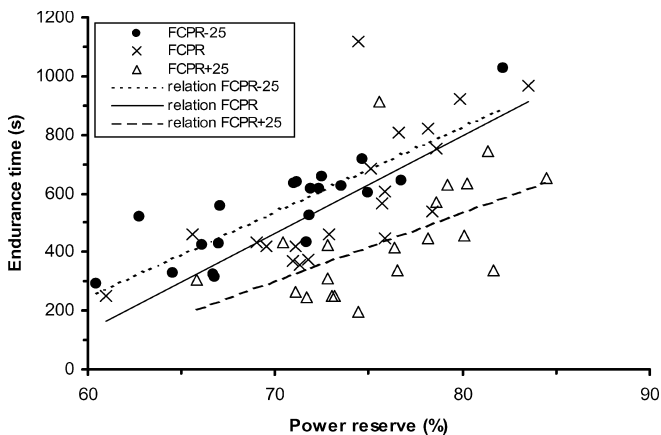


Fig. 4 Relationship between power reserve and endurance time at each of the three endurance sessions. All relations are significant and the equations of the regression lines are: Endurance time at $\dot{W}90_{FCPR-25} = 28.8(\text{power reserve at } \dot{W}90_{FCPR-25}) - 1480$, endurance time at $\dot{W}90_{FCPR} = 33.2(\text{power reserve at } \dot{W}90_{FCPR}) - 1858$ and endurance time at $\dot{W}90_{FCPR+25} = 23.3(\text{power reserve at } \dot{W}90_{FCPR+25}) - 1329$, with r -values of 0.85 ($P < 0.01$), 0.73 ($P < 0.01$), and 0.56 ($P < 0.01$), respectively

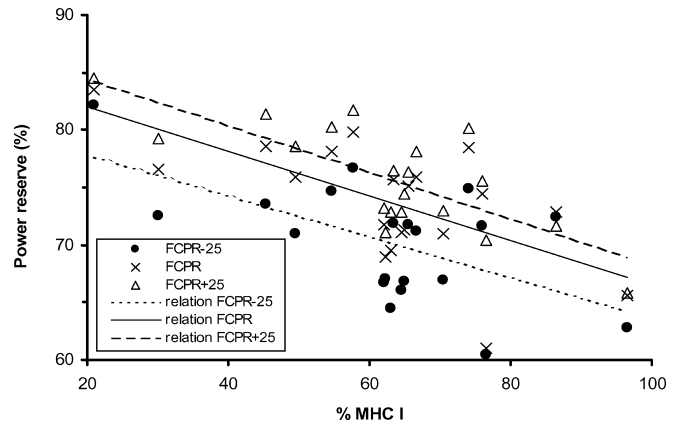


Fig. 5 Relationship between the percentage of slow twitch muscle fibres (% MHC I) and power reserve at each of the endurance sessions. All relations are significant and the equations of the regression lines are: Power reserve at $\dot{W}90_{FCPR-25} = -0.20(\% \text{ MHC I}) + 88.6$, power reserve at $\dot{W}90_{FCPR} = -0.19(\% \text{ MHC I}) + 85.9$, and power reserve at $\dot{W}90_{FCPR+25} = -0.18(\% \text{ MHC I}) + 81.4$, with r -values of -0.76 ($P < 0.01$), -0.65 ($P < 0.01$) and -0.59 ($P < 0.01$), respectively

pendent variables revealed significant relationships at $\dot{W}90_{FCPR-25}$ ($r = 0.86$), $\dot{W}90_{FCPR}$ ($r = 0.73$) and $\dot{W}90_{FCPR+25}$ ($r = 0.56$). Still, in these multiple regression analyses only power reserve turned out to correlate significantly with endurance time.

Discussion

The main result of the present study was the longer endurance time during high intensity cycling at FCPR, compared with the pedalling rate 25% higher than FCPR. Further, no difference was seen in endurance time between cycling at FCPR and 25% below this. These results were accompanied by the finding that metabolic responses, such as $\dot{V}O_2$ and blood lactate concentration, were generally higher at FCPR + 25 than at FCPR and FCPR-25, whether measurements were made after 5 min or at exhaustion. Statistically significant differences were also found between metabolic responses at FCPR-25 and FCPR. However, because of the small magnitude of these differences they may be considered not to be of physiological significance. Altogether, these results partially support the hypothesis described in the introduction that a group of subjects, during cycling at high exercise intensity, achieve the best endurance performance when cycling is performed at FCPR, compared with higher pedalling rates. However, lower pedalling rates resulting in minimum energy turnover seem to be equally successful with regard to endurance time. The merging at high exercise intensity of FCPR and the pedalling rate that results in minimum energy turnover may be the reason for the finding that subjects in the present study achieved the longest endurance times when cycling at FCPR or FCPR-25, compared with FCPR + 25. In this context it should be

noted that the present results cannot be extended to low or moderate exercise intensities because, at such sub-maximal levels, FCPR, relatively speaking, is considerable higher than the pedalling rate resulting in minimum energy turnover.

The mechanism responsible for the faster development of fatigue during cycling at the highest pedalling rate in the present study was probably associated with high energy turnover, as supported by the higher metabolic response at this cycling condition compared to the two other conditions. Another mechanism responsible for development of fatigue during cycling may be associated with high mechanical work demand, like performance of high muscle force. If this latter mechanism was responsible for development of fatigue it was most likely during cycling at the lowest pedalling rate applied. The reason for this is the increased force to be applied to the pedal as pedalling rate decreases (Böning et al. 1984; Hansen et al. 2002a; Takaishi et al. 1998). However, since endurance time was similar at FCPR-25 and FCPR, it is speculated that an even lower pedalling rate than FCPR-25 should have been applied to demonstrate high mechanical work demand as a limiting factor in prolonged high intensity cycling.

Interestingly, the present study showed that endurance time was negatively related to $\dot{V}O_{2\max}$. Thus, the lower the $\dot{V}O_{2\max}$ the better the endurance performance, despite this being in contrast to what might be intuitively expected. The reason for this finding relates to the experimental design of the present study, in which the subjects performed cycling at the same exercise intensities relative to $\dot{V}O_{2\max}$. As a consequence, higher $\dot{V}O_{2\max}$ resulted in higher W_{90} or, in other words, in higher absolute mechanical work demand. Further, since mechanical capacities of subjects, such as maximal peak crank power, were unrelated to their $\dot{V}O_{2\max}$, the relative mechanical work demand was highest for the subjects with the highest $\dot{V}O_{2\max}$, possibly causing their endurance time to be shorter.

Of further interest, the present study showed endurance time to be negatively related to % MHC I. Thus, lower percentages of slow twitch muscle fibres resulted in better endurance performance. This contrasted a previous study (Horowitz et al. 1994) where the researchers compared the highest sustainable power output during a 1-h endurance performance test of two groups of cyclists: one with a high and one with a normal % MHC I. The cyclists with a high percentage of slow twitch fibres produced the highest power output. However, in that study, in contrast to the present study, the total group of subjects demonstrated only a small variation in $\dot{V}O_{2\max}$. Further, subjects from the two groups were matched for $\dot{V}O_{2\max}$, for statistical analysis. In the present study, the negative relationship between % MHC I and endurance time may simply reflect the previously discussed negative relationship between $\dot{V}O_{2\max}$ and endurance time, since % MHC I was related to $\dot{V}O_{2\max}$. Thus, the relative mechanical work demand was highest for the subjects with the highest % MHC I.

In further support of this, it was previously reported that, for the subjects in the present study, % MHC I was negatively related to the mechanical capacity of maximal peak crank power (Hansen et al. 2002a).

Endurance time was related to power reserve at all three pedalling rates applied. Thus, the higher the power reserve the better the endurance performance, speaking on the individual level. It is worth noting that power reserve at all three pedalling rates applied was negatively related to % MHC I, which was in agreement with the negative relationship between endurance time and % MHC I, as previously discussed.

It is possible that differences in muscle fibre type recruitment, as affected by differences in mechanical capacities and work demands, affected the endurance time. For example, it may be speculated that subjects with a low compared to a high power reserve needed to recruit a larger fraction of fast twitch muscle fibres in order to be able to cope with the mechanical work demand. It has been suggested that fast twitch muscles fibres generate work less efficiently during cycling (Coyle et al. 1992; Hansen et al. 2002a), which is generally thought to be disadvantageous during prolonged exercise. In support of this speculation, it has previously been shown that cycling at a power output corresponding to 85% of $\dot{V}O_{2\max}$ with 50 and 100 rpm resulted in a larger fast twitch fibre glycogen depletion at 50 rpm where the power reserve is smaller (Ahlquist et al. 1992).

Multiple regression analyses were performed with endurance time as the dependent variable and with variables related to physiological capacities ($\dot{V}O_{2\max}$ and power reserve) as independent or predictor variables. However, this type of analysis did not increase the proportion of variance in the dependent variable that can be attributed to the variance in the predictor variables. The reason was that the predictor variables correlated with each other to a certain extent and thus, to a degree, explained the same variation in the dependent variable. Only one (power reserve) contributed significantly to the regression when they were used in combination.

On basis of the present study it appears that one way to improve the endurance performance in cycling for those subjects who performed the poorest at a relatively high level of intensity could involve improving their power reserve via strength and power training. However, it should be emphasised that if the endurance performance at an absolute level (instead of at a relative level as in the present study) of high intensity cycling was to be improved, (e.g. the finishing time in a short time trial), the training should also aim to improve a physiological capacity like $\dot{V}O_{2\max}$.

In conclusion, the present study investigated endurance performance during high intensity cycling for a group of subjects with a large inter-subject variation in muscle fibre type composition. By analysing data on a group level our hypothesis regarding longer endurance time at FCPR compared to a pedalling rate 25% higher

than FCPR was confirmed. However, this was not the case for a pedalling rate 25% lower than FCPR, since endurance time at this pedalling rate was similar to that at FCPR. Metabolic responses, such as $\dot{V}O_2$ and blood lactate concentration, generally were higher at FCPR + 25 than at FCPR - 25 and FCPR. These results were in support of the hypothesis that, for a group of subjects, cycling at minimum energy turnover results in the best endurance performance. Further, inter-individual physiological variables were of significance, e.g. endurance time was negatively related to $\dot{V}O_{2max}$, $\dot{W}90$, and % MHC I, but positively related to power reserve. These results suggested that, on the individual level, strength and power training for improvement of mechanical capacities such as power reserve could be advantageous, since cycling at a relatively low mechanical work demand may result in the best endurance performance.

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