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ORIGINAL ARTICLE

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Cycling efficiency and pedalling frequency in road cyclists

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Abstract The purpose of this study was to determine the influence of pedalling rate on cycling efficiency in road cyclists. Seven competitive road cyclists participated in the study. Four separate experimental sessions were used to determine oxygen uptake ($\dot{V}O_2$) and carbon dioxide output ($\dot{V}CO_2$) at six exercise intensities that elicited a $\dot{V}O_2$ equivalent to 54, 63, 73, 80, 87 and 93% of maximum $\dot{V}O_2$ ($\dot{V}O_{2max}$). Exercise intensities were administered in random order, separated by rest periods of 3–5 min; four pedalling frequencies (60, 80, 100 and 120 rpm) were randomly tested per intensity. The oxygen cost of cycling was always lower when the exercise was performed at 60 rpm. At each exercise intensity, $\dot{V}O_2$ showed a parabolic dependence on pedalling rate ($r = 0.99$–1, all $P < 0.01$) with a curvature that flattened as intensity increased. Likewise, the relationship between power output and gross efficiency (GE) was also best fitted to a parabola ($r = 0.94$–1, all $P < 0.05$). Regardless of pedalling rate, GE improved with increasing exercise intensity ($P < 0.001$). Conversely, GE worsened with pedalling rate ($P < 0.001$). Interestingly, the effect of pedalling cadence on GE decreased as a linear function of power output ($r = 0.98$, $n = 6$, $P < 0.001$). Similar delta efficiency (DE) values were obtained regardless of pedalling rate [21.5 (0.8), 22.3 (1.2), 22.6 (0.6) and 23.9 (1.0)%, for the 60, 80, 100 and 120 rpm, mean (SEM) respectively]. However, in contrast to GE, DE increased as a linear function of pedalling rate ($r = 0.98$, $P < 0.05$). The rate at which pulmonary ventilation increased was accentuated for the highest pedalling rate ($P < 0.05$), even after accounting for differences in exercise intensity and $\dot{V}O_2$ ($P < 0.05$). Pedalling rate per se did not have any influence on heart rate which, in turn, increased linearly with $\dot{V}O_2$. These results may help us to understand why competitive cyclists often pedal at cadences of 90–105 rpm to sustain a high power output during prolonged exercise.

Key words Exercise · Gross efficiency · Delta efficiency · Performance · Lactate

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Introduction

The ratio between mechanical work and the energy consumed to do the work is defined as mechanical efficiency (Winter 1990), whilst the ratio between oxygen uptake ($\dot{V}O_2$) and power output is known as economy. Work efficiency has been defined as the ratio between external mechanical work (i.e. the work done on the load) and the metabolic cost of the exercise after discounting the metabolic cost of zero-work or cost measured with the cyclist freewheeling (Winter 1990). Superior efficiency (or economy) is associated with higher levels of performance in various sports (López Calbet et al. 1993; Coyle 1995). Paradoxically, even though the most economical pedalling frequencies for stationary cycling lie between 50 and 80 rpm (Gaesser and Brooks 1975; Coast and Welch 1985), road cyclists prefer to use pedalling rates of 90–105 rpm during prolonged exercise at high intensities (Hagberg et al. 1981; Horowitz et al. 1994; Sargeant 1994). A similar behaviour has been described in non-cyclists (Takaishi et al. 1998). Several theories have been proposed to explain this preference for high pedal cadences, including minimising stress and fatigue (Patterson et al. 1983; Patterson and Moreno 1990; Takaishi et al. 1996), reducing glycogen depletion (Ahlquist et al. 1992) and optimising the application of forces on the pedals (Ericson and Nisell 1988; Kautz et al. 1991; Sanderson 1991; Rådemaker et al. 1994). However, none of these explanations provides a definitive answer to the question of why cyclist and non-cyclists select a pedalling rate that is apparently less efficient.

The amount of energy released per litre of oxygen consumed depends upon the substrate oxidized. Therefore, it is preferable to transform $\dot{V}O_2$ values into energy expended to calculate the efficiency of muscle contraction, rather than simply measuring the economy of movement. The efficiency of muscular contraction reflects the product of phosphorylation efficiency with which chemical energy from carbohydrate and fat is converted to adenosine triphosphate, and the contraction-coupling efficiency with which the energy released during ATP hydrolysis is converted in mechanical energy through muscle shortening (Whipp and Wasserman 1969). In general, efficiency measures are based on the assessment whole-body $\dot{V}O_2$, which includes the oxygen cost of muscle contraction during pedalling plus the oxygen consumed by other tissues, such as the heart and the respiratory muscles. During cycling, leg and whole-body $\dot{V}O_2$ show parallel increments (Poole et al. 1992). Poole et al. (1992) demonstrated that estimates of muscular efficiency calculated from whole-body $\dot{V}O_2$ approximate very well the efficiency of working limb muscles during cycling.

So far, most studies have focussed on the analysis of gross efficiency (GE) or the ratio between external work and total energy consumption, because it is relatively easy to measure and does not include any uncertainty due to base-line correction for resting $\dot{V}O_2$ or for zero-load pedalling (work efficiency; Gaesser and Brooks 1975; Stainsby et al. 1980). However, it has been suggested that delta efficiency (DE), the ratio of the change in work accomplished and the change in energy expended, is a more useful indicator of performance in road cyclists (Coyle et al. 1992; Horowitz et al. 1994; Coyle 1995) since there is a strong relationship between DE and the percentage of type I fibres, as well as between the percentage of type I fibres and endurance (Coyle et al. 1992; Horowitz et al. 1994; Coyle 1995). Despite the fact that DE gives a valuable estimate of the relative energy cost of performing an additional increment of work (Stainsby et al. 1980), it must be acknowledged that neither GE nor DE can be considered as valid measures of actual muscular efficiency (Stainsby et al. 1980).

As far as we know, there is no clear picture about the influence that pedalling rate might have on DE. While Gaesser and Brooks (1975) reported a decrease in DE with pedalling rate, others have found an increase (Böning et al. 1984; Sidossis et al. 1992). Part of this controversy may be attributable to differences in the range of pedalling rates and cycling intensities analysed, as well as differences in the procedures used to calculate DE.

Therefore, the main purpose of this study was to ascertain whether the adoption of high pedalling frequencies by road cyclists can be explained in terms of differences in cycling efficiency, especially DE, at various pedalling rates and exercise intensities. Another purpose was to determine whether the increase in $\dot{V}O_2$ that is associated with increasing pedalling rate can be accounted for by changes in the cardiorespiratory and metabolic responses to exercise. That is, to find out whether or not there is a tight coupling between the $\dot{V}O_2$, pulmonary ventilation ($\dot{V}_E$) and blood lactate concentration ([La]) when exercising at the same intensity but using different pedalling frequencies.

Methods

Subjects

Seven competitive road cyclists participated in this study. Their physical characteristics are reported in Table 1. All of the subjects had been participating in national amateur competitions for at least the last 3 years. The subjects were requested to follow similar diets and reduce their level of physical activities during the 48 h prior to the experiments. They were also instructed to refrain from ingesting any food for at least 4 h before each session. Before volunteering, each subject was fully informed of the purposes, protocol and procedures of this experiment, and any associated risks.

Experimental procedures

Subjects completed six laboratory sessions over a 4-weeks period. During the 1st week, they were accustomed to the experimental protocol and their maximal $\dot{V}O_2$ ($\dot{V}O_{2max}$) and the exercise intensity at which $\dot{V}O_{2max}$ occurred (W_{max}) was measured twice, on separate days, using incremental exercise tests until exhaustion, with increments of 20 and 30 W/min, at 80–90 rpm (Ergo-metrics 900). Ventilatory and gas exchange variables were monitored breath-by-breath, and averaged every 15 s by an open-circuit sampling system (CPX, Medical Graphics, St. Paul, Minnesota, USA). The metabolic cart was calibrated with calibration gas mixtures of known oxygen and carbon dioxide concentrations (accuracy 0.01%), which were provided by the manufacturer (CPX, Medical Graphics). In our laboratory, $\dot{V}O_2$ and carbon dioxide output ($\dot{V}CO_2$) during submaximal cycling have been assessed with a coefficient of variation of lower than 5%, as well as with an intraclass reliability coefficient higher than 0.98, as determined in six physical education students at four different intensities on 4 different days. The highest $\dot{V}O_2$ value attained during either of the incremental exercise tests was taken as the $\dot{V}O_{2max}$.

Table 1 General physical characteristics, and performance achieved during the incremental exercise with steps of 20 $W \cdot min^{-1}$ and 30 $W \cdot min^{-1}$. Values are given as means (SEM). ($\dot{V}O_{2max}$, Maximal oxygen uptake, W_{max} intensity at which $\dot{V}O_{2max}$ occurred, HR_{max} maximal heart rate, *NS* not significant)

Characteristic	Value	Incremental exercise tests		
		20 $W \cdot min^{-1}$	30 $W \cdot min^{-1}$	*P*
Age (years)	23.5 (1.2)			
Height (cm)	169 (3)			
Body mass (kg)	60.5 (3.4)			
$\dot{V}O_{2max}$ ($l \cdot min^{-1}$)		4.1 (0.2)	4.1 (0.2)	NS
W_{max} (W)		371 (15)	374 (15)	NS
HR_{max} (beats $\cdot min^{-1}$)		192 (4)	185 (5)	<0.01

Subsequently, four separate experimental sessions were used to determine the $\dot{V}O_2$ and $\dot{V}CO_2$ at six exercise intensities that elicited a $\dot{V}O_2$ equivalent to 54, 63, 73, 80, 87 and 93% of $\dot{V}O_{2max}$. Exercise intensities were administered in a random order, and were separated by rest periods of 3–5 min. Four pedalling frequencies (60, 80, 100 and 120 rpm) were randomly tested per intensity, on different experimental days. To reduce thermal stress and minimise water losses due to sweating, subjects were fan cooled and ingested 100 ml of water during the resting periods. Tests were performed at 20–24°C, ≈70% relative humidity and 740–750 mmHg atmospheric pressure. The duration of each exercise bout was restricted to 6 min. The $\dot{V}O_2$ and $\dot{V}CO_2$ for each exercise intensity is given by the mean of the last 2 min of the exercise bout.

Finally [La] was assessed during the 5th min of exercise, from capillary blood obtained from the ear lobe, previously hyperaemised with Finalgon. [La] was determined in whole blood using a lactate analyser (YSI 1500 Sport, Yellow Springs, Colo., USA) equipped with a haemolysing agent (Triton X100). Blood lactate measurements were only performed at two exercise intensities, 54% and 93% of $\dot{V}O_{2max}$.

Calculations

GE was calculated as the ratio of work accomplished · min^{-1} to energy expended · min^{-1}, using the $\dot{V}O_2$ and energy equivalent for oxygen corresponding to each respiratory exchange ratio value from the tables of Péronnet and Massicotte (1991). DE, the ratio of the change in work accomplished · min^{-1} and the change in energy expended · min^{-1}, was assessed for each individual at each pedalling rate, from a linear regression ($y = a + bx$) of the relationship between energy expended versus work accomplished (5–6 points). Then, DE was calculated as the reciprocal of the slope of this relationship (i.e. 1/b). Exercise intensities for which [La] was greater than 4 mM were not included in DE calculations.

Statistical analysis

Differences between pedalling rates and exercise intensities were assessed using analysis of variance for repeated measures (four rates × six intensities). Tukey's HSD post hoc tests were conducted in the event of statistically significant F-ratios ($P < 0.05$). To relate $\dot{V}O_2$ to power, individual regression equations were derived by least square linear fit for each pedalling rate. Likewise, non-linear regression analysis was used to describe the relationship between $\dot{V}O_2$, $\dot{V}_E$, heart rate (HR) and [La] as dependent variables and pedalling rate as an independent variable. An analysis of covariance (ANCOVA; SPSS, Chicago, Ill., USA) was performed with $\dot{V}O_2$ as a covariate to assess whether the effects of pedalling rate on GE, ventilatory variables and HR were attributable to differences in $\dot{V}O_2$. Due to some high [La] values at the highest exercise intensity, ANCOVA analysis was circumscribed to the first five intensities. The level of statistical significance was set at $P \leq 0.05$. Data are presented as means (SEM).

Results

$\dot{V}O_2$ and cycling efficiency

Similar values for $\dot{V}O_{2max}$ and W_{max} were obtained in both incremental exercise tests (Table 1). In each subject, $\dot{V}O_2$ increased linearly with exercise intensity at each pedalling rate ($r = 0.98$–1, $P < 0.05$). However, as depicted in Fig. 1a, the higher the pedalling frequency, the lower the slope of the $\dot{V}O_2$-power output relationship ($P < 0.001$). For a given exercise intensity, $\dot{V}O_2$ showed a parabolic dependence upon pedalling rate ($r = 0.99$–1, all $P < 0.01$) such that $\dot{V}O_2$ increased with pedalling rate

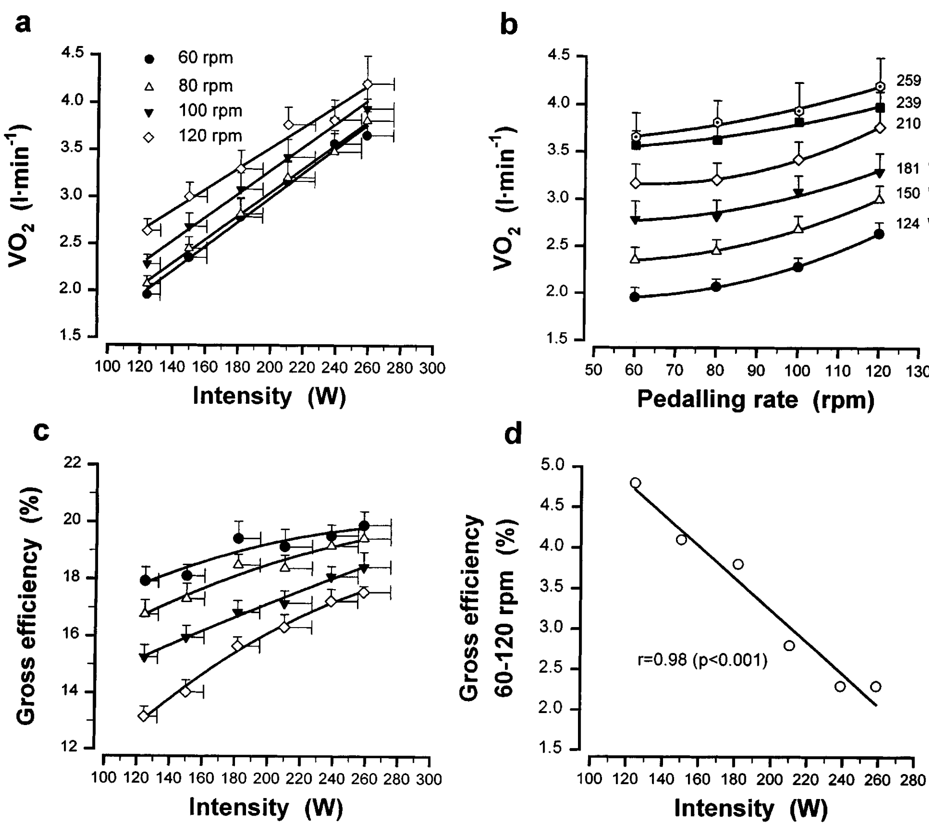

Fig. 1a–d **a** The relationship between oxygen uptake ($\dot{V}O_2$) and exercise intensity when cycling at different pedalling rates. **b** The relationship between $\dot{V}O_2$ and pedalling rate when cycling at each of six different exercise intensities. Each point represents the mean (± SEM) value for seven cyclists. **c** Relationship between gross efficiency and exercise intensity when cycling at different pedalling rates. **d** Mean difference in gross efficiency between 60 and 120 rpm versus exercise intensity

(Fig. 1b). Interestingly, the curvature of the $\dot{V}O_2$/pedalling rate relationship flattened as intensity increased, even though the oxygen cost of cycling was always lower when the exercise was performed at 60 rpm.

Likewise, the relationship between power output and GE was also best fitted to a parabola ($r=0.94$–1, all $P < 0.05$; Fig. 1c). Regardless of pedalling rate, GE improved with increasing exercise intensity ($P < 0.001$). Conversely, GE worsened as a function of pedalling rate ($P < 0.001$). In addition, for a given $\dot{V}O_2$, GE was greater for the slower pedalling frequencies (Fig. 5a). The maximal value of GE [19.9 (0.7)%] was reached when subjects cycled at a relative intensity of 93% of $\dot{V}O_{2max}$ using a pedalling rate of 80 rpm. In contrast, the smallest GE [13.2 (0.4)%] was recorded during cycling bouts performed at the lowest exercise intensity and the fastest pedalling rate (Fig. 1c). The mean difference in GE between 60 and 120 rpm was 4.8, 4.1, 3.8, 2.8, 2.3 and 2.3%, for 124, 150, 181, 210, 239 and 259 W, respectively. The effect of pedalling cadence on GE decreased as a linear function of power output ($r=0.98$, $n=6$, $P < 0.001$; Fig. 1d). Furthermore, from this relationship it can be predicted that a similar GE will be achieved at 367 W, for 60 and 120 rpm.

Similar values of DE were obtained regardless of pedalling rate [21.5 (0.8), 22.3 (1.2), 22.6 (0.6) and 23.9 (1.0)%, for 60, 80, 100 and 120 rpm, respectively]. However, in contrast to GE, DE increased as a linear function of pedalling rate ($r=0.98$, $P < 0.05$; Fig. 2).

Blood lactate concentration

As depicted in Fig. 3a, [La] was not affected by pedalling rate at the lowest exercise intensity. However, at the highest exercise intensity, [La] increased with pedalling frequency, following a parabolic pattern ($r=0.98$, $P < 0.01$). Similar [La] values were observed at the highest cycling intensity when the pedalling rate was lower than 120 rpm [3.9 (0.5), 4.4 (0.5) and 4.6 (0.4) mM, for 60, 80 and 100 rpm, respectively]. In contrast, at 120 rpm [La] increased markedly, reaching 6.5 (0.3) mM ($P < 0.05$, compared with the other pedalling rates). In addition, when the mean [La] values were plotted against the $\dot{V}O_2$ elicited by each pedalling frequency, the [La] response was found to closely follow a parabolic function (Fig. 3b).

Ventilatory variables and HR

As can be seen in Fig. 4, both HR and $\dot{V}_E$ increased with exercise intensity ($P < 0.001$). For a given intensity, HR and $\dot{V}_E$ increased with pedalling rate, following a para-

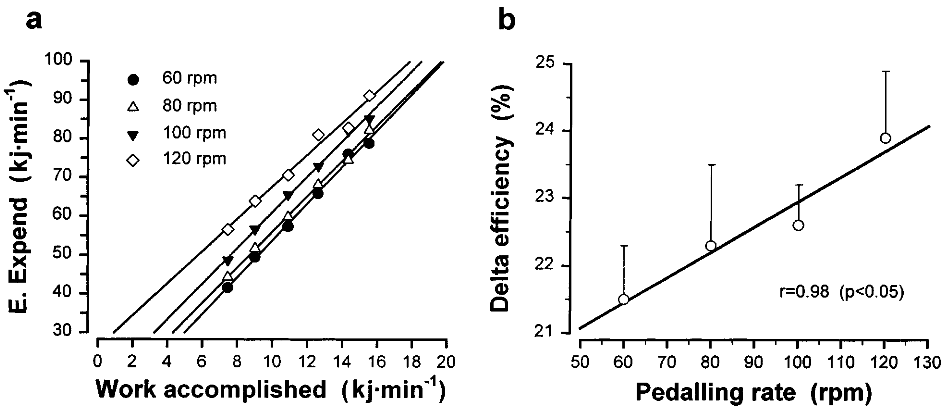

Fig. 2a, b **a** The relationship between energy expended (E. Expended) and work accomplished (external) when cycling at different pedalling rates. **b** The delta efficiency and pedalling rate in revolutions per minute (rpm). Each point represents the mean (± SEM) value of seven cyclists

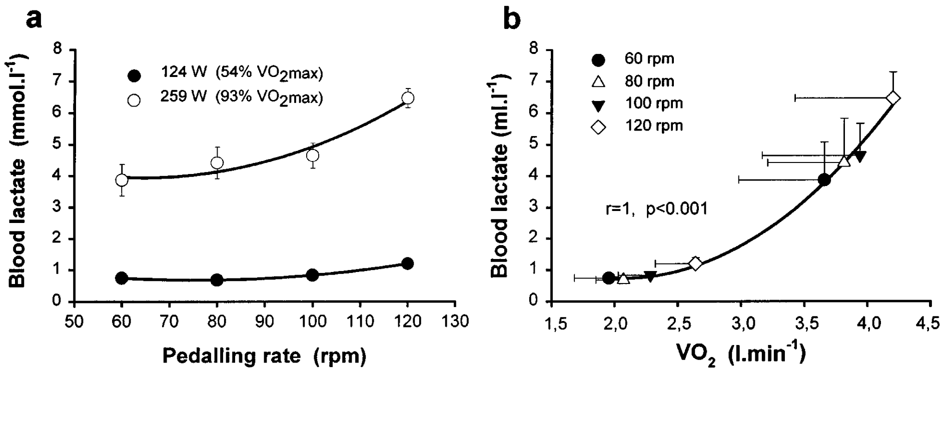

Fig. 3a, b Blood lactate response to exercise at intensities of 124 W (*closed circles*) and 259 W (*open circles*). **a** Relationship between blood lactate and pedalling rate. **b** Blood lactate response plotted versus $\dot{V}O_2$. Each point represents the mean (± SEM) value of seven cyclists

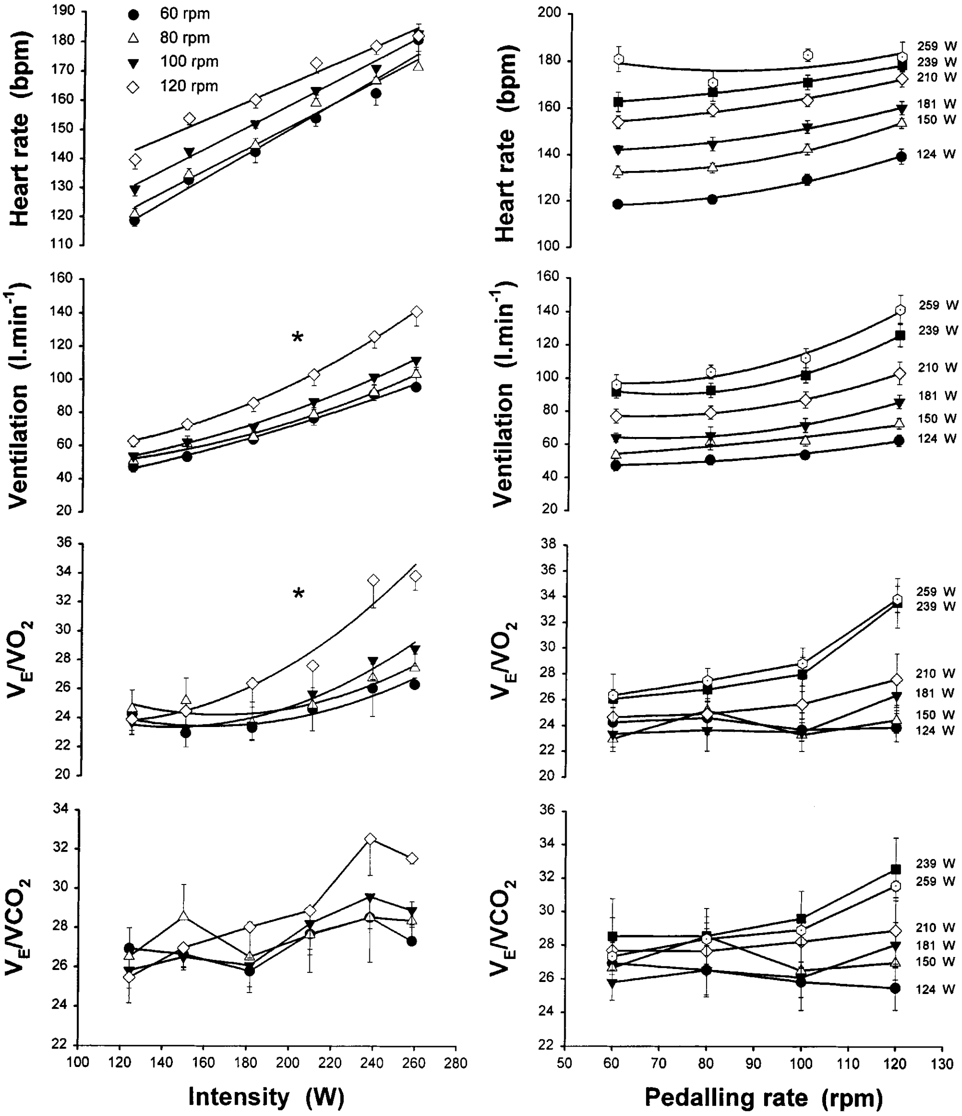

Fig. 4 Cardiorespiratory variables measured during exercise at different intensities and pedalling rates. ($\dot{V}_E/\dot{V}O_2$ Ventilatory equivalent for oxygen, $\dot{V}_E/\dot{V}CO_2$ ventilatory equivalent for carbon dioxide). Each point represents the mean ($\pm$SEM) value of seven cyclists. *Significant difference between pedalling at 120 rpm and the three other pedalling frequencies

bolic function (all $r > 0.98$, $P < 0.05$). In addition, the rate at which $\dot{V}_E$ increased was accentuated at the highest pedalling rate ($P < 0.05$; Fig. 5c). The ventilatory equivalent for oxygen ($\dot{V}_E/\dot{V}O_2$) increased with both pedalling rate ($P < 0.05$) and cycling intensity ($P < 0.001$). Consequently, for a given $\dot{V}O_2$, the greatest $\dot{V}_E/\dot{V}O_2$ was elicited by the fastest pedalling rate ($P < 0.05$) (Figs. 4 and 5d). In contrast, the ventilatory equivalent for carbon dioxide ($\dot{V}_E/\dot{V}CO_2$) was not affected by pedalling rate (Figs. 4 and 5e).

Discussion

The principal finding of this study is that DE increases with pedalling rate in road cyclists. In contrast, GE deteriorates with increasing pedalling frequency. However, for a given pedalling frequency, GE improves as power output increases. Since the relationship between GE and exercise intensity is also parabolic, and since the curvature of this relationship is attenuated as the exercise intensity is increased, the effect of pedalling rate on GE is reduced as exercise intensity is increased.

The principal advantage of DE is that it provides a more valid estimate of the true muscular efficiency than does GE, since the change in energy expended is calculated relative to the change in actual work accomplished, which discounts more of the metabolic processes that do not contribute to the actual work accomplished (Whipp and Wasserman 1969; Gaesser and Brooks 1975; Stainsby et al. 1980; Coyle et al. 1992). Consequently, DE is expected to give greater efficiencies than GE, as confirmed by the results of the present study. The DE values reported are similar to those obtained previously for road cyclists (Coyle et al. 1992; Sidossis et al. 1992) and active, non-cyclist subjects (Gaesser and Brooks 1975; Kang et al. 1997). Previous investigations have shown that DE increases with pedalling frequency for rates between 40 and 100 rpm (Böning et al. 1984), as well as between 60 and 100 rpm (Sidossis et al. 1992). It

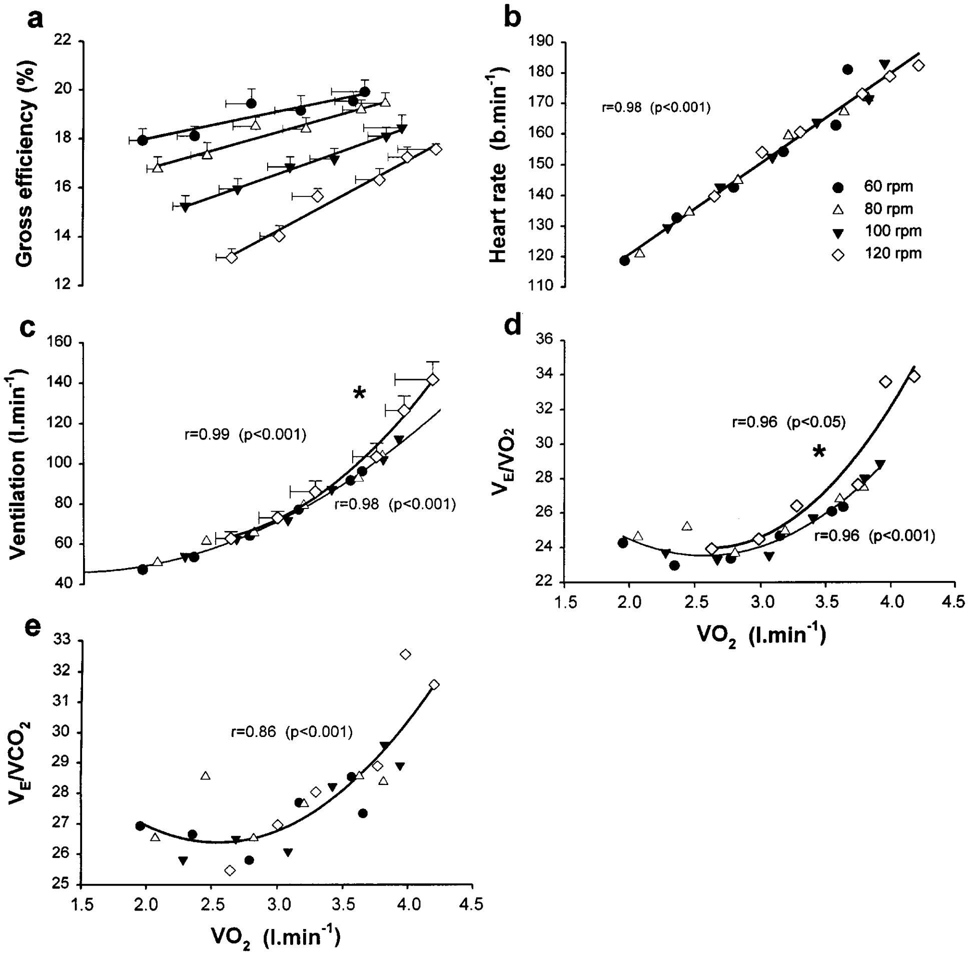

Fig. 5a–e The relationship between gross efficiency (**a**), heart rate (**b**), ventilation (**c**), $\dot{V}_E/\dot{V}O_2$ (**d**), and $\dot{V}_E/\dot{V}CO_2$ (**e**), and $\dot{V}O_2$. Each point represents the mean value (SEM) of seven cyclists. *Significant difference between pedalling at 120 rpm and the three other pedalling frequencies

is noteworthy that our study confirms these results and demonstrates that DE improves linearly with pedalling rate at frequencies between 60 and 120 rpm (2–3%, in efficiency units). In contrast, Gaesser and Brooks (1975) reported that DE decreased with pedalling rates between 40 and 100 rpm in non-cyclists. However, a quite different way of calculating DE was used by Gaesser and Brooks (1975). On the other hand, since DE is either maintained (Kang et al. 1997) or declines with cycling intensity (Stuart et al. 1981; Böning et al. 1984) it would be advantageous to elevate pedalling frequency when the workload is increased since, according to our data, DE will be improved with pedalling rate. Although the magnitude of this improvement will be small, it might influence markedly performance during moderate- to high-intensity prolonged road cycling.

Our results are in accordance with the work of Coast and Welch (1985) and Böning et al. (1984), who also observed a parabolic relationship between $\dot{V}O_2$ and pedalling rate in cyclists. Other investigators have also reported a curvilinear relationship between $\dot{V}O_2$ and pedalling rate (Seabury et al. 1977; Löllgen et al. 1980; Böning et al. 1984; Takaishi et al. 1998). Interestingly, the effect of pedalling rate on $\dot{V}O_2$ was reduced at high power outputs (Böning et al. 1984). Some authors have provided evidence for the existence of an optimum pedalling rate (i.e. a pedalling rate at which $\dot{V}O_2$ reaches a minimum while power output is maintained). Markedly different values for optimum pedalling rate have been reported, but the majority of authors have obtained values lying between 45 and 90 rpm (McKay and Banister 1976; Seabury et al. 1977; Löllgen et al. 1980; Hagberg et al. 1981; Patterson et al. 1983; Böning et al. 1984; Coast and Welch 1985; Takaishi et al. 1998). In general, the studies showing lower optimum pedalling frequencies used lower power outputs (Seabury et al. 1977; Takaishi et al. 1998) than those who reported the greatest optimum pedalling rates (Hagberg et al. 1981). Coast and Welch (1985) reported that the optimum pedalling frequency increases linearly with power output in cyclists. Such a finding has not been confirmed in the present study, where the lowest $\dot{V}O_2$ was consistently registered at the slowest pedalling rate tested, that is at 60 rpm. Nevertheless, in agreement with our results, other investigators have also found the lowest $\dot{V}O_2$ at pedalling cadences close to 60 rpm, even at high power outputs (McKay and Banister 1976; Seabury et al. 1977; Böning et al. 1984; Takaishi et al. 1998). In fact, the linear relationship between $\dot{V}O_2$ and optimum pedalling rate reported by Coast and Welch (1985) is questionable, since these investigators always obtained the lowest $\dot{V}O_2$ at 60 rpm, regardless of exercise intensity (see Fig. 1 of Coast and Welch 1985).

Obviously, GE values will increase if the denominator of the ratio of work output to energy expended is reduced, or if the numerator is increased. Mechanical work during cycling can be considered as the sum of the external work (work done on the load) plus the internal work (work done on the body segments). The latter, unfortunately, can only be estimated roughly, by applying complex biomechanical models that must deal with the incertitude about inter-segmental transfer, storage and dissipation of energy (Winter 1990; Neptune and van den Bogert 1998). The cyclist performs internal work just to move his limbs through the pedal revolution, even when the external load is zero (Winter 1990). Therefore, at the same external load, GE would be lower for high cadences if internal work increases with pedalling rate, just because the numerator would be underestimated, since it does not account for internal work. The relative contribution from this source will diminish as external mechanical work increases, because it becomes proportionally less. As mentioned previously, GE could also increase with exercise intensity if the magnitude of the denominator diminishes. In fact, the contribution of resting $\dot{V}O_2$ to the whole-body $\dot{V}O_2$ will be smaller the greater the absolute value of $\dot{V}O_2$ elicited by the muscle contractions. Thus, GE may be improving with exercise intensity, as observed in the present study and in others (Gaesser and Brooks 1975; Kang et al. 1997; Stuart et al. 1981; Böning et al. 1984) due, in great part, to a reduction in the relative contribution of other tissues to whole-body $\dot{V}O_2$ and, although less likely, to a reduction of energy cost of muscle contraction with exercise intensity. In theory, some of these problems could be circumvented by using DE as an estimate of true mechanical efficiency (Gaesser and Brooks 1975; Coyle et al. 1992; Horowitz et al. 1994; Coyle 1995).

Since for a given workload $\dot{V}O_2$ increases with pedalling rate, it was considered interesting to examine the effect of pedalling rate per se on GE at different workloads. Thus, ANCOVA analysis with $\dot{V}O_2$ and pedalling rate as covariates was applied. Significant differences in GE across workloads were still detectable after accounting for differences in $\dot{V}O_2$ and pedalling frequency. As depicted in Fig. 5a, the higher GE was always attained at the slowest pedalling rate, regardless of $\dot{V}O_2$. Nonetheless, it must be highlighted that the slope of the GE/$\dot{V}O_2$ relationship was steepest for the fastest pedalling rate (i.e. 120 rpm), which implies that the improvement in GE with increasing exercise intensity was accentuated for the fastest pedalling rate. Consequently, pedalling-rate-induced differences in GE are lower at high intensities.

Our results are also supported by in vitro experiments that emphasise the interdependence between the efficiency of muscle contraction and the velocity of shortening (Goldspink 1978; Crow and Kushmerik 1982; Heglund and Cavagna 1987). For example, Heglund and Cavagna (1987) showed that the efficiency of mammalian and the frog skeletal muscles contracting under in vitro conditions increases with the speed of contraction, until reaching a maximum, which corresponds to the optimal velocity of shortening. In addition, muscles composed predominantly of slow-twitch fibres are more efficient than predominantly fast-twitch muscles, over the full range of contraction speeds, when the comparison is made at the same percentage of the maximal shortening velocity (Heglund and Cavagna 1987). However, when slow and fast muscles contract at the same absolute speed, fast muscles are more efficient at high speeds and, conversely, slow muscle are more efficient at slow speeds (Suzuki 1979; Heglund and Cavagna 1987; Sargeant 1994). Both fatigue of type I fibres during prolonged exercise and increases in exercise intensity require the additional recruitment of type II fibres to sustain the power output (Beelen and Sargeant 1993; Rome 1993; Sargeant 1994). Therefore, to maintain (or even increase) efficiency under these conditions, the pedalling rate would have to be shifted to higher pedalling frequencies. In theory, such a strategy could facilitate improvements in performance.

Nonetheless, increasing the pedalling rate might also enhance whole-body $\dot{V}O_2$, since for a given $\dot{V}O_2$ the ventilatory response was higher at the fastest pedalling rate (see Fig. 5c, d). Consequently, the oxygen cost of breathing increases at the fastest pedalling frequencies. The oxygen cost of $\dot{V}_E$ can be assumed to lie between 1.8 and 2.85 ml $\cdot$ l^{-1} at the exercise intensities examined in this study (Aaron et al. 1992). Therefore, the repercussion of changes in $\dot{V}_E$ on whole-body $\dot{V}O_2$, when switching from 60 to 120 rpm, would only account for 2–3% (at 124 W) and 8–13% (at 259 W) of the difference in $\dot{V}O_2$ measured at pedal cadences of between 60 and 120 rpm. This implies that the contribution of the oxygen cost of $\dot{V}_E$ to the increase in whole-body $\dot{V}O_2$ when changing from 60 to 120 rpm increases with exercise intensity.

The reason why $\dot{V}_E$ is elevated is less apparent, but at least two mechanisms can be suggested. Firstly, at the highest exercise intensity, [La] approached 4 mM, and even exceeded this value, when pedalling at 120 rpm (see Fig. 2). Despite the fact that the relative contribution of glycolysis to energy yield at these exercise intensities is probably very low in trained cyclists (Coyle et al. 1988), a slight increase in $\dot{V}CO_2$ would be expected to occur, as a result of lactic acid buffering (Wasserman 1987). Consequently, additional delivery of carbon dioxide to the central circulation would further stimulate $\dot{V}_E$ (Wasserman et al. 1986). This explanation is supported by a similar response of $\dot{V}_E/\dot{V}CO_2$ across pedalling rates, when $\dot{V}_E/\dot{V}CO_2$ was plotted against $\dot{V}O_2$. Secondly, a neurogenic-mediated stimulus, central or peripheral in origin, might have evoked supplementary ventilatory drive (Takano 1988). Such a mechanism would have to be accompanied by an non-linear increase in $\dot{V}_E/\dot{V}CO_2$ with pedalling rate, especially in the absence of lactic acidosis. However, $\dot{V}_E/\dot{V}CO_2$ was barely affected by pedalling rate at low intensities (i.e. at loads for which [La] was unchanged).

Finally, this study showed that there was a tight linear coupling between HR and $\dot{V}O_2$ that was not distorted by pedalling rate; thus, superimposable straight lines characterised the HR/$\dot{V}O_2$ relationship for each pedalling frequency. From this observation it may be hypothesised that HR, in contrast to $\dot{V}_E$, is an index of exercise intensity that is not affected by pedalling rate.

In summary, this study has shown that DE increases as a linear function of pedalling rate in road cyclists, despite the fact that high pedalling rates are associated with hyperventilation which, in turn, increases the oxygen cost of $\dot{V}_E$, and therefore whole-body $\dot{V}O_2$. In contrast, the heart's response to cycling is tightly coupled to $\dot{V}O_2$, independently of pedalling rate. These results may help us to understand why competitive cyclists often pedal at cadences of 90–105 rpm to sustain high power outputs during prolonged exercise. The role that DE might play in determining performance deserves further attention.

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