

## Effect of internal power on muscular efficiency during cycling exercise

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**Abstract** The purpose of this study was to investigate the muscular efficiency during cycling exercise under certain total power output ( $P_{\text{tot}}$ ) or external power output ( $P_{\text{ext}}$ ) experimental conditions that required a large range of pedal rates from 40 to 120 rpm. Muscular efficiency estimated as a ratio of  $P_{\text{tot}}$ , which is sum of internal power output ( $P_{\text{int}}$ ) and  $P_{\text{ext}}$ , to rate of energy expenditure above a resting level was investigated in two experiments that featured different conditions on a cycle ergometer, which were carried out at the same levels of  $P_{\text{tot}}$  (Exp. 1) and  $P_{\text{ext}}$  (Exp. 2). Each experiment consisted of three exercise tests with three levels of pedal rates (40, 80 and 120 rpm) lasting for 2–3 min of unloaded cycling followed by 4–5 min of loaded cycling.  $\dot{V}\text{O}_2$  during unloaded cycling ( $\sim 430 \text{ ml min}^{-1}$  for 40 rpm,  $\sim 640 \text{ ml min}^{-1}$  for 80 rpm,  $\sim 1,600 \text{ ml min}^{-1}$  for 120 rpm) and the  $P_{\text{int}}$  ( $\sim 3 \text{ W}$  for 40 rpm,  $\sim 25 \text{ W}$  for 80 rpm,  $\sim 90 \text{ W}$  for 120 rpm) in the two experiments were markedly increased with increasing pedal rates. The highest muscular efficiency was found at 80 rpm in the two experiments, whereas a remarkable reduction (19%) in muscular efficiency obtained at 120 rpm could be attributable to greater  $\text{O}_2$  cost due to higher levels of  $P_{\text{int}}$  accompanying the increased pedal rates. We concluded that muscular efficiency could be

affected by the differences in  $\text{O}_2$  cost and  $P_{\text{int}}$  during cycling under the large range of pedal rates employed in this study.

**Keywords** Pedal rate · Metabolic cost · Oxygen uptake · Noncontractile processes · Muscle fiber type

### Introduction

Efficiency of exercising muscle during steady state exercise is defined as the ratio of power output to rate of energy expenditure (Gaesser and Brooks 1975). In many previous studies (Gaesser and Brooks 1975; Coyle et al. 1992; Hansen et al. 2002; Horowitz et al. 1994; Mogensen et al. 2006), external power output ( $P_{\text{ext}}$ ) has been used as an index of power output during exercise, which refers to the application of force through a distance either by a muscle or by an intact body (Stainsby et al. 1980). On the other hand, exercising muscle generates not only  $P_{\text{ext}}$  but also internal power output ( $P_{\text{int}}$ ), defined as the power performed on the body segments (Cavagna and Kaneko 1977; Hansen et al. 2004), which implies that the expended energy above a resting level could be attributable to both  $P_{\text{ext}}$  and  $P_{\text{int}}$  during exercise. Therefore, total power output ( $P_{\text{tot}}$ ) including  $P_{\text{int}}$  and  $P_{\text{ext}}$  as the power output generated by exercising muscle should be taken into consideration when estimating “muscular efficiency” at different contraction frequencies, to avoid the underestimation of actual power output during muscle contractions given by  $P_{\text{ext}}$  only (Ferguson et al. 2000). In previous studies based on quantification of  $P_{\text{int}}$ , muscular efficiency has been reported to range from 21 to 30% (Ferguson et al. 2002; Hansen and Sjøgaard 2006; Luhtanen et al. 1987). This variation is thought to derive from the differences of contraction

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velocity and exerted force in the exercising muscle, even when the same evaluation method is used to measure muscular efficiency. In addition the same method for estimation of  $P_{\text{int}}$  was not used in these studies. Thus, this could also explain some of the difference.

$P_{\text{int}}$  was estimated by measuring mechanical and metabolic energy changes in various biomechanical and physiological models (Minetti et al. 2001; Sjøgaard et al. 2002; Wells et al. 1986; Willems et al. 1995; Winter 1979). It has been reported that  $P_{\text{int}}$  exponentially increases as a function of pedal rate during cycling and that oxygen uptake ( $\dot{V}O_2$ ) also exponentially increases with increasing pedal rates above a given higher pedal rate, even under the same level of  $P_{\text{ext}}$  (Coast and Welch 1985; Foss and Hallén 2004; Seabury et al. 1977), suggesting greater  $O_2$  cost and  $P_{\text{int}}$  at higher pedal rates. This means that muscular efficiency would be affected by greater  $O_2$  cost due to higher levels of  $P_{\text{int}}$  with increasing pedal rates. However, there has been no study that investigated muscular efficiency during cycling based on estimation of  $P_{\text{int}}$  in a large range of pedal rates. We hypothesized in this study that muscular efficiency could decrease at higher pedal rates during cycling exercise and that lower muscular efficiency could be caused by higher  $O_2$  cost with increasing pedal rate.

The purpose of this study was to investigate the muscular efficiency during cycling exercise under certain  $P_{\text{tot}}$  or  $P_{\text{ext}}$  experimental conditions that required a large range of pedal rates from 40 to 120 rpm.

## Methods

### Subjects

Seven healthy male subjects (age  $22.4 \pm 0.4$  years; height  $169.6 \pm 1.9$  cm; mass  $64.1 \pm 2.9$  kg,  $\dot{V}O_{2\text{max}}$ ;  $43.6 \pm 2.9$  ml  $\text{kg}^{-1} \text{min}^{-1}$ ) volunteered to participate in experiment 1 (Exp. 1) and nine healthy male subjects (age  $20.7 \pm 0.8$  years; height  $170.3 \pm 1.6$  cm; mass  $62.6 \pm 1.6$  kg,  $\dot{V}O_{2\text{max}}$ ;  $47.8 \pm 2.1$  ml  $\text{kg}^{-1} \text{min}^{-1}$ ) in experiment 2 (Exp. 2). All subjects were physically active, but none was specifically trained. They were all informed of the purpose and procedure of this study, and gave their informed, written consent prior to testing. The experimental protocol used in this study was approved by the Ethics Committee for Human Subjects of the Kyushu Institute of Technology.

### Experimental protocol

This study consisted of two experiments with different cycling conditions; Exp. 1 and Exp. 2 were carried out at

the same levels of  $P_{\text{tot}}$  and  $P_{\text{ext}}$ , respectively (Table 1). In each experiment the subjects performed three exercise tests with different pedal rates (40, 80 and 120 rpm) on a friction-braked cycle ergometer (Monark 818E, Crescent AB, Sweden). The load during cycling at each pedal rate was adjusted to maintain the same  $P_{\text{tot}}$  level in Exp. 1 and the same  $P_{\text{ext}}$  level in Exp. 2, since  $P_{\text{int}}$  and  $P_{\text{ext}}$  were expected to alter with the changes in pedal rates. The exercise tests were composed of 3-min rest and unloaded cycling for 2 min followed by 5-min loaded cycling in Exp. 1, and 3-min rest and unloaded cycling for 3 min followed by 4-min loaded cycling in Exp. 2. An electrical metronome was set to assist subjects in maintaining the target pedal rates. The three exercise tests in each experiment were carried out in randomized order separated from a recovery period ( $\sim 30$  min) within 1 day.

### Measurements

Breath-by-breath pulmonary gas exchange parameters were measured continuously throughout the exercise tests using a metabolic analysis system (A-E 300S, Minato Medical Science, Japan). Inspired and expired gas volumes were measured using a hot-wire respiratory-flow system. The expired fractions of oxygen ( $O_2$ ) and carbon dioxide ( $CO_2$ ) were analyzed using a paramagnetic oxygen-analyzer and an infrared carbon dioxide analyzer, respectively. The system was calibrated prior to each test according to the manufacturer's instructions. The volume was calibrated before each test by manually pumping a 2-l syringe. The  $O_2$  and  $CO_2$  analyzers were calibrated using a standard gas of known concentration ( $O_2$  15.01%,  $CO_2$  5.020% in  $N_2$  balance) before each test. Breath-by-breath minute ventilation ( $\dot{V}_E$ ),  $O_2$  uptake ( $\dot{V}O_2$ ),  $CO_2$  output ( $\dot{V}CO_2$ ) and respiratory exchange ratio ( $R$ ;  $\dot{V}CO_2/\dot{V}O_2$ ) were determined, and the data were stored on a hard disk for future analyses. Heart rate (HR) was recorded telemetrically with a Polar heart rate monitor (S610i, Polar Electro Oy, Finland). Pulmonary gas exchange parameters and HR data were averaged for 1 min (from first to second min) in a sitting position on the ergometer and during unloaded cycling exercise, and for 2 min (last 2 min) during loaded cycling exercise.

Arterialized capillary blood samples were taken from the fingertip immediately before and after each exercise test, and blood lactate concentration was analyzed by a semi-automated lactate analyzer (YSI-1500 Sport, Yellow Springs Ins., USA).

Flywheel frequency during cycling was measured by an IC hall sensor attached to the cycle ergometer to analyze pedal frequency.

**Table 1** Target power outputs at three target pedal rates in two experiments

|                             | Exp. 1   |          |           | Exp. 2   |          |           |
|-----------------------------|----------|----------|-----------|----------|----------|-----------|
|                             | 40 (rpm) | 80 (rpm) | 120 (rpm) | 40 (rpm) | 80 (rpm) | 120 (rpm) |
| Target $P_{\text{int}}$ (W) | 3        | 23       | 78        | 3        | 23       | 77        |
| Target $P_{\text{ext}}$ (W) | 105      | 84       | 29        | 59       | 59       | 59        |
| Target $P_{\text{tot}}$ (W) | 108      | 107      | 108       | 62       | 82       | 135       |

$P_{\text{int}}$  internal power output,  $P_{\text{ext}}$  external power output,  $P_{\text{tot}}$  total power output, *Exp. 1* exercise tests under same total power output level, *Exp. 2* exercise tests under same external power output level

## Calculations

Total energy expenditure ( $\dot{E}_{\text{tot}}$ ) was calculated as the sum of aerobic energy expenditure ( $\dot{E}_{\text{aerobic}}$ ) plus anaerobic energy expenditure ( $\dot{E}_{\text{anaerobic}}$ ).  $\dot{E}_{\text{aerobic}}$  was calculated using the  $R$  and  $\dot{V}\text{O}_2$  at a steady state level from the following equation based on a table developed by Lusk (1924):

$$\dot{E} \text{ (W)} = (1.232R + 3.815) \dot{V}\text{O}_2 (1 \text{ min}^{-1}) / 0.0143.$$

$\dot{E}_{\text{anaerobic}}$  (W) was estimated by substitution of  $\dot{V}\text{O}_2$  derived from blood lactate accumulation ( $[\Delta\text{La}]$ ) into the above equation. The  $\dot{V}\text{O}_2$  was estimated from conversion of the  $[\Delta\text{La}]$  ( $\text{mmol l}^{-1}$ ) calculated as the difference between pre- and post-exercise lactate concentration from the following equation (Di Prampero and Ferretti 1999):

$$\dot{V}\text{O}_2 (\text{ml min}^{-1}) = 3.3 [\Delta\text{La}] \text{ BM (body mass; kg)}.$$

The exercising muscle performs both  $P_{\text{ext}}$  and  $P_{\text{int}}$  (Cavagna and Kaneko 1977).  $P_{\text{ext}}$  was estimated from external (pedal) force and pedal frequency ( $f$ ; Hz) that was calculated by actually measured flywheel frequency and the ratio of pedal to flywheel rotations (3.64).

$$P_{\text{ext}} \text{ (W)} = \text{load (kp)} 9.8 (\text{m s}^{-2}; \text{gravitational acceleration}) \times 6 (\text{m rev.}^{-1}) f \text{ (Hz)}.$$

According to Minetti et al. (2001),  $P_{\text{int}}$  was estimated from BM and  $f$  as follows:

$$P_{\text{int}} \text{ (W)} = 0.153 \text{ BM (kg)} f^3 \text{ (Hz)}.$$

Muscular efficiency was calculated by dividing the total power output ( $P_{\text{tot}} = P_{\text{int}} + P_{\text{ext}}$ ) by the energy expenditure above a resting state (Kaneko et al. 1979; Ferguson et al. 2002; Hansen and Sjøgaard 2006). In this study the  $P_{\text{tot}}$  was used as an index of power output generated by exercising muscle, because our main purpose was to investigate the effect of muscular efficiency under different levels of pedal rates and/or  $P_{\text{int}}$  during cycling. We used the following equation:

$$\text{Muscular efficiency (\%)} = (P_{\text{int}} + P_{\text{ext}}) / (\dot{E}_{\text{tot}} - \dot{E}_{\text{rest}}) \times 100\%$$

where  $\dot{E}_{\text{tot}}$  was total energy expenditure during loaded cycling and  $\dot{E}_{\text{rest}}$  energy expenditure at a resting state.

## Statistics

All data are presented as means  $\pm$  SEM. A one-way ANOVA with repeated measures was used to test the differences in physiological variables between the three exercise tests in each experiment. If a significant  $F$  ratio was obtained, then a Student–Newman–Keuls post hoc test was performed to obtain the differences in the selected variables. A Pearson's correlation coefficient was employed to test the relationship between two variables. Statistical significance was accepted at  $P < 0.05$ .

## Results

Cardio-respiratory variables ( $\dot{V}\text{O}_2$ ,  $R$  and HR),  $[\Delta\text{La}]$ , actually measured pedal rates, power output ( $P_{\text{int}}$ ,  $P_{\text{ext}}$  and  $P_{\text{tot}}$ ) and energy expenditures ( $\dot{E}_{\text{aerobic}}$  and  $\dot{E}_{\text{anaerobic}}$ ) during unloaded and loaded cycling exercise at three levels of pedal rates in two experiments are given in Table 2. In two experiments  $\dot{V}\text{O}_2$  during unloaded cycling revealed the highest values (1,560–1,600  $\text{ml min}^{-1}$ ) at 120 rpm compared with 40 rpm (370–430  $\text{ml min}^{-1}$ ) and 80 rpm (630–640  $\text{ml min}^{-1}$ ). As a result of the increased  $P_{\text{int}}$ ,  $\dot{V}\text{O}_2$  was observed to rise with increasing pedal rate regardless of  $P_{\text{ext}} = 0$ . Similarly,  $[\Delta\text{La}]$  at 120 rpm was also significantly higher than 80 rpm for Exp. 1, and 40 and 80 rpm for Exp. 2, respectively ( $P < 0.05$ ). The estimated  $P_{\text{int}}$  at 120 rpm ( $\sim 90$  W) was markedly increased with increasing pedal rate ( $\sim 3$  W at 40 rpm and  $\sim 25$  W at 80 rpm) in the two experiments.

In Exp. 1 under the same level of  $P_{\text{tot}}$ , the difference between the measured and target pedal rates was found to be larger at 120 rpm than at the other two pedal rates. Consequently, the  $P_{\text{int}}$  showed a higher value at 120 rpm

**Table 2** Cardio-respiratory variables, blood lactate accumulation, measured pedal rate, power outputs and energy expenditures during cycling exercise at three levels of pedal rates under two experimental conditions

|   | Exp. 1      |               |              | Exp. 2      |                |              |
|---|-------------|---------------|--------------|-------------|----------------|--------------|
|   | 40 (rpm)    | 80 (rpm)      | 120 (rpm)    | 40 (rpm)    | 80 (rpm)       | 120 (rpm)    |
| $\dot{V}O_{2\text{unloaded}}$ (ml min <sup>-1</sup> ) | 432 ± 31    | 644 ± 46***   | 1,567 ± 96*  | 373 ± 12    | 630 ± 18***    | 1,602 ± 42*  |
| $\dot{V}O_{2\text{loaded}}$ (ml min <sup>-1</sup> )   | 1,626 ± 64  | 1,424 ± 70*** | 1,829 ± 101* | 998 ± 10    | 1,178 ± 17***  | 2,061 ± 59*  |
| $R_{\text{unloaded}}$                                 | 0.86 ± 0.01 | 0.83 ± 0.02** | 0.93 ± 0.02* | 0.91 ± 0.02 | 0.87 ± 0.02**  | 0.96 ± 0.03  |
| $R_{\text{loaded}}$                                   | 0.97 ± 0.03 | 0.96 ± 0.02** | 1.01 ± 0.02* | 0.84 ± 0.02 | 0.90 ± 0.02*** | 1.02 ± 0.02* |
| $HR_{\text{unloaded}}$ (beat min <sup>-1</sup> )      | 92 ± 3      | 93 ± 3**      | 142 ± 3*     | 77 ± 2      | 86 ± 3***      | 133 ± 5*     |
| $HR_{\text{loaded}}$ (beat min <sup>-1</sup> )        | 133 ± 4     | 125 ± 4**     | 156 ± 3*     | 103 ± 3     | 109 ± 5**      | 152 ± 6*     |
| [ $\Delta La$ ] (mmol l <sup>-1</sup> )               | 1.4 ± 0.5   | 1.0 ± 0.3**   | 2.3 ± 0.5    | 0.9 ± 0.2   | 1.0 ± 0.2**    | 3.4 ± 0.3*   |
| $MPR_{\text{unloaded}}$ (rpm)                         | 43 ± 0.5    | 84 ± 1.0      | 126 ± 0.6    | 43 ± 0.3    | 83 ± 0.6       | 127 ± 0.5    |
| $MPR_{\text{loaded}}$ (rpm)                           | 41 ± 0.3    | 82 ± 0.2      | 126 ± 0.3    | 41 ± 0.2    | 82 ± 0.2       | 124 ± 0.4    |
| $P_{\text{int}}$ (W)                                  | 3 ± 0.2     | 25 ± 1.1***   | 90 ± 4.1*    | 3 ± 0.1     | 24 ± 0.6***    | 84 ± 1.8*    |
| $P_{\text{ext}}$ (W)                                  | 109 ± 3.0   | 86 ± 3.7***   | 31 ± 0.1*    | 60 ± 0.2    | 60 ± 0.2       | 61 ± 0.2     |
| $P_{\text{tot}}$ (W)                                  | 113 ± 3.2   | 110 ± 4.7**   | 121 ± 4.1*   | 63 ± 0.3    | 85 ± 0.7***    | 145 ± 1.8*   |
| $\dot{E}_{\text{aerobic}}$ (W)                        | 478 ± 18    | 401 ± 20***   | 546 ± 32*    | 254 ± 6     | 316 ± 9***     | 639 ± 21*    |
| $\dot{E}_{\text{anaerobic}}$ (W)                      | 23 ± 9      | 16 ± 4**      | 38 ± 9       | 15 ± 3      | 18 ± 4**       | 61 ± 6*      |

$\dot{V}O_{2\text{unloaded}}$  oxygen uptake during unloaded cycling,  $\dot{V}O_{2\text{loaded}}$  oxygen uptake during loaded cycling,  $R_{\text{unloaded}}$  respiratory exchange ratio during unloaded cycling,  $R_{\text{loaded}}$  respiratory exchange ratio during loaded cycling,  $HR_{\text{unloaded}}$  heart rate during unloaded cycling,  $HR_{\text{loaded}}$  heart rate during loaded cycling, [ $\Delta La$ ] blood lactate accumulation,  $MPR_{\text{unloaded}}$  measured pedal rate during unloaded cycling,  $MPR_{\text{loaded}}$  measured pedal rate during loaded cycling,  $P_{\text{int}}$  internal power output,  $P_{\text{ext}}$  external power output,  $P_{\text{tot}}$  total power output, *Exp. 1* exercise tests under same total power output level, *Exp. 2* exercise tests under same external power output level

\* Significantly different from 40 rpm in same experiment. \*\* Significantly different from 120 rpm in same experiment

for Exp. 1 than that for Exp. 2, and thus  $P_{\text{tot}}$  calculated as the sum of  $P_{\text{int}}$  and  $P_{\text{ext}}$  was significantly higher at 120 rpm (121 ± 4.1 W) in a comparison with 40 rpm (113 ± 3.2 W) and 80 rpm (110 ± 4.7 W) ( $P < 0.05$ ).  $\dot{E}_{\text{tot}}$  calculated during cycling at 80 rpm (418 ± 23 W) was significantly lower compared to that at 40 rpm (502 ± 20 W) and 120 rpm (584 ± 39 W) ( $P < 0.05$ ). Due to the lower levels of  $P_{\text{tot}}$  and  $\dot{E}_{\text{tot}}$ , muscular efficiency estimated at 80 rpm (26.5 ± 0.8%) was significantly higher than that at 40 rpm (22.6 ± 0.8%) and at 120 rpm (21.1 ± 1.0%) ( $P < 0.05$ , Fig. 1, upper panel).

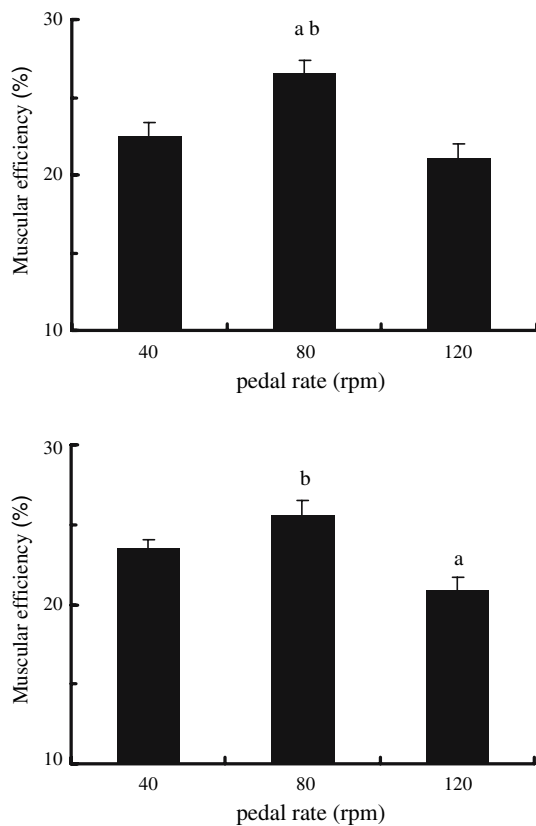
In Exp. 2 under the same level of  $P_{\text{ext}}$ , the actually measured  $P_{\text{ext}}$  showed a similar value in three exercise tests at three levels of pedal rates. However, muscular efficiency at 120 rpm (20.9 ± 0.9%) was significantly lower than that at 40 (23.5 ± 0.5%) and 80 rpm (25.6 ± 0.9%) ( $P < 0.05$ , Fig. 1, lower panel).

## Discussion

The main finding obtained in the present study was that there was an inverted U shaped relationship between pedal rate and muscular efficiency and that the highest muscular efficiency (approximately 26%) was found at 80 rpm and the lowest muscular efficiency at 120 rpm in both

experiments (Fig. 1). Luhtanen et al. (1987) have demonstrated that efficiency values assessed from the same experimental data, based on several definitions of efficiency, were 19.7–17.4% for gross efficiency ( $P_{\text{ext}}/\dot{E}_{\text{tot}}$ ), 21.8–17.5% for net efficiency [ $P_{\text{ext}}/(\dot{E}_{\text{tot}} - \dot{E}_{\text{rest}})$ ] and 29.7–21.0% for muscular efficiency [ $(P_{\text{int}} + P_{\text{ext}})/(\dot{E}_{\text{tot}} - \dot{E}_{\text{rest}})$ ] in a cycling exercise from light to heavy exercise intensities. This finding would imply that the estimation of efficiency is influenced by how energy expenditure consumed by and power output generated by exercising muscle itself are evaluated. Therefore, the evaluations for these variables during exercise must be precisely made under various exercise conditions such as different pedal rates. In both experiments of the present study the estimated  $P_{\text{int}}$  was markedly increased with increasing pedal rate (Table 2).

An estimation of  $P_{\text{int}}$  in this study was made using the equation proposed by Minetti et al. (2001). Although various models have been developed for estimating  $P_{\text{int}}$ , consistent methods and criteria for the assessment of  $P_{\text{int}}$  have not yet been obtained. Sjøgaard et al. (2002) proposed an independent estimation of  $P_{\text{int}}$  based on metabolic data to reevaluate whether the computation of  $P_{\text{int}}$  is justified. We found that the calculation from pedal rate and body mass proposed by Minetti et al. (2001) could be easily applied for the estimation of  $P_{\text{int}}$  in cycling. Hansen et al.



**Fig. 1** Muscular efficiency as a function of pedal rate during cycling exercise at three levels of pedal rates in experiment 1 (*upper panel*) and 2 (*lower panel*). *a* Significantly different from 40 rpm, *b* significantly different from 120 rpm

(2004) compared  $P_{\text{int}}$  from the different models and showed that  $P_{\text{int}}$  from Minetti's model (2001) was lower than that from other models. We therefore inferred that  $P_{\text{int}}$  evaluated by the model of Minetti et al. (2001) in this study might be underestimated. However, when considering small differences of  $P_{\text{int}}$  between physiological and biomechanical models, it seems unlikely that the slightly lower estimation of  $P_{\text{int}}$  in this study could affect significantly the present results of muscular efficiencies. Ferguson et al. (2002) estimated  $P_{\text{int}}$  from the model of Minetti et al. (2001) to investigate the influence of pedal rate and muscle temperature on muscular efficiency. A correlation coefficient between  $P_{\text{int}}$  estimated from the present data using both the Minetti et al. (2001) and Sjøgaard et al. (2002) models was 0.95 ( $P < 0.001$ ), indicating that the estimated  $P_{\text{int}}$  level would be adequate. Furthermore, the muscular efficiency obtained in our two experiments was observed to range from 20.9 to 26.5%, which is consistent with the values reported by the previous studies using similar methods for estimation of muscular efficiency as we used in this study (Ferguson et al. 2002; Hansen and Sjøgaard 2006; Luhtanen et al. 1987).

A possible explanation for the present result is that  $\dot{V}O_2$  exponentially increases with increasing pedal rate. In fact, we observed that  $\dot{V}O_2$  and  $P_{\text{int}}$  increased remarkably with increasing pedal rate during unloaded cycling, as shown in Table 2. The magnitude of  $\dot{V}O_2$  appears to change depending on the levels of  $P_{\text{int}}$ . This is supported by previous studies that examined  $\dot{V}O_2$  as a function of optimal pedal rate.  $\dot{V}O_2$  at a given power output ( $P_{\text{ext}}$ ) during cycling was minimized at a unique pedal rate (60–80 rpm) and exponentially increased from the pedal rate (Coast and Welch 1985; Foss and Hallén 2004; Seabury et al. 1977), while MacIntosh et al. (2000) illustrated the same feature with electromyogram (EMG) data. This means that optimal muscular efficiency could exist in a unique pedal rate and decrease with increasing pedal rate, which is consistent with the present results that higher muscular efficiency existed at 80 rpm and decreased with increasing pedal rate.

Our results raised a question about why  $O_2$  cost would be larger at higher pedal rates. This would be due to extra energy related to energy turnover by the  $Ca^{2+}$ -ATPase for noncontractile processes at higher cycling pedal rates (Abbate et al. 2001; Baker et al. 1994). Energy released from ATP is converted into power outputs including  $P_{\text{int}}$  and  $P_{\text{ext}}$ , and is also used by various ion pumps, particularly the  $Ca^{2+}$  pump of the sarcoplasmic reticulum (SR) (Barclay 1994). Blinks et al. (1978) demonstrated that  $Ca^{2+}$  reabsorption into the SR further increased at higher contraction frequencies. On the other hand, it has been reported that a large proportion ( $\sim 43\%$ ) of ATP is used by noncontractile processes, with more ATP derived from anaerobic rather than aerobic metabolism (Baker et al. 1994). This notion is consistent with the present data that larger  $[\Delta La]$  was observed at 120 rpm compared with 40 and 80 rpm (Table 2), which would lead to more anaerobic energy at 120 rpm, resulting in lower muscular efficiency. Hogan et al. (1998) demonstrated that muscle contractions of short duration resulted in a significantly higher calculated rate of ATP utilization, a threefold increase in glycolysis and greater fatigue related to the increased intracellular  $[La^-]$  and  $[H^+]$ , compared with muscle contractions of long duration in canine muscle. It is possible that the lower muscular efficiency as a consequence of higher energy expenditure at the higher pedal rate might be related to noncontractile processes such as excessive energy consumption related to the reaccumulation of  $Ca^{2+}$  by the SR.

The muscular efficiency at 40 rpm was significantly lower than that at 80 rpm in Exp. 1, but there was no significant difference in Exp. 2 compared with efficiency at 80 rpm. Human skeletal muscle is composed mainly of type I and type II muscle fibers. Furthermore, the ratio of the two fiber types in the recruited muscle fibers is altered by tension exerted in exercising muscle or by exercise

intensity (Sargeant 1994). Type II muscle fibers are more inefficient than type I muscle fibers in humans (Coyle et al. 1992; Jones et al. 2004; Hansen et al. 2002; Horowitz et al. 1994; Mogensen et al. 2006). Ahlquest et al. (1992), using the same experimental condition as our Exp. 1, demonstrated that at the same metabolic rate glycogen depletion in type II muscle fibers at 50 rpm was greater than that at 100 rpm during cycling. This means that a greater recruitment of type II muscle fibers at the lower pedal rate could be induced due to higher muscle force required to overcome the higher resistance per cycle at the same metabolic rate. The lower muscular efficiency at the lower pedal rate with higher pedal force may result from the greater recruitment of low-efficiency type II muscle fibers, presumably owing to the higher muscle force exerted. This supports the results of Exp. 1 that muscular efficiency at a lower pedal rate (40 rpm) with higher pedal force (250%↑) was significantly lower than that at 80 rpm under the same  $P_{\text{tot}}$  condition.

In conclusion, there was an inverted *U* shaped relationship between pedal rate and muscular efficiency during cycling exercise under certain  $P_{\text{tot}}$  or  $P_{\text{ext}}$  experimental conditions that required a large range of pedal rates. Muscular efficiency could be affected by the differences in  $O_2$  cost and  $P_{\text{int}}$  due to the levels of pedal rates.

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