

EFFECT OF SWITCHING PEDAL RATE MODEL ON SLOW COMPONENT OF OXYGEN UPTAKE DURING HEAVY-CYCLE EXERCISE

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Abstract. We examined the effect of a change in the muscle fiber recruitment patterns on the occurrence of the VO_2 slow component ($\text{VO}_{2\text{SC}}$) using both a previously employed exercise model for maintaining a given pedal rate (60 rpm:60con or 110 rpm:110con) throughout constant-load exercise and a newly designed exercise model for switching the pedal rate at the halfway point (60→110 rpm:60→110swi or 110→60 rpm:110→60swi) during constant-metabolic demand cycling exercise. Seven healthy male volunteers [mean \pm SD: age 24 \pm 2 years, body mass 64.8 \pm 7.5 kg] performed four square-wave transitions at work rates calculated from each relationship between the oxygen uptake and the work rate obtained in two incremental cycling tests with 60 rpm and 110 rpm. The work rates were set to require a VO_2 at the ventilatory threshold (VT) plus a VO_2 equal to 50% of the difference between the VT and the peak VO_2 (50% Δ). Both pulmonary gas exchange parameters and surface electromyogram (EMG) were measured during all transition exercises. VO_2 above rest (ΔVO_2) divided by the total mechanical power output (W_{tot} = external + internal power outputs) ($\Delta\text{VO}_2/W_{\text{tot}}$), which was estimated as an index for the oxygen cost per unit of all work accomplished in 60→110swi and 110→60swi, showed either a decrease or an increase concomitant with the switching pedal rates, respectively. Similarly, the integrated EMG (iEMG) after the halfway point of the exercise tests tended to decrease for 60→110swi and increase for 110→60swi, respectively. From the results of this study ($\Delta\text{VO}_2/W_{\text{tot}}$ and iEMG responses), it is inferred that the exercise model designed in this study may induce a change in the muscle fiber recruitment pattern from the halfway point during constant-metabolic demand exercise. However, no differences were observed in the amplitude of the $\text{VO}_{2\text{SC}}$ among the four trials, thus indicating that a change in the muscle fiber recruitment pattern is therefore not closely related to the appearance of $\text{VO}_{2\text{SC}}$ during constant-metabolic demand cycling exercise. Therefore, we believe that some

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other factors exist in the exercising muscle which is responsible for the induction of $\dot{V}O_{2SC}$.

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Key words: Pedal rate - EMG - Mechanical power output - Oxygen cost

Introduction

During heavy constant-load exercise above the lactate threshold (LT), the pulmonary oxygen uptake ($\dot{V}O_2$) does not reach a steady state and continue to rise slowly [14]. The slower increase in $\dot{V}O_2$ during heavy constant-load exercise is widely acknowledged as the slow component ($\dot{V}O_{2SC}$) [27].

The phenomenon of the $\dot{V}O_{2SC}$ has been accounted for a number of mechanisms including increased oxygen costs of ventilatory and cardiac muscle work, endocrine effects, lactate clearance, an elevated body temperature and the additional oxygen cost of the exercising muscle [22]. Although the direct evidence underlying $\dot{V}O_{2SC}$ has not been yet shown, it has been widely acknowledged that a main source of $\dot{V}O_{2SC}$ originates from the exercising limbs [23]. A strong candidate for inducing $\dot{V}O_{2SC}$ is a greater recruitment of the exercising muscle fibers, especially a progressive recruitment of low-efficiency type II muscle fibers [4,7,26] according to an earlier study indicating that type II muscle fibers produce more heat and consume more oxygen [9].

Barstow *et al.* [4] and Pringle *et al.* [25] compared the amplitudes of the $\dot{V}O_{2SC}$ between different pedal rates at the same metabolic demand using an exercise model for maintaining a given pedal rate throughout exercise, indicating that the $\dot{V}O_{2SC}$ occurred at the later phase (2~3 min) of constant-load exercise. Although their exercise protocol would induce the different muscle fiber recruitment from onset of exercise between the different pedal rates, it would be raised whether a change in muscle fiber recruitment would occur at the later phase during exercises. Therefore, these studies seem unlikely to reveal the cause and effect relationship between the occurrence of $\dot{V}O_{2SC}$ (at the later phase during exercise) and the muscle fibers recruitment pattern (at the onset of exercise). To determine the obvious cause and effect between them, a new exercise model should thus be developed. The new exercise model for switching the pedal rate at the halfway point during cycling exercise, which would induce a change in the muscle fiber recruitment patterns concomitant with switching the pedal rate, could give us new insight for a better understanding of the occurrence of $\dot{V}O_{2SC}$ during constant-load exercise.



The present study was therefore to examine the effect of a change in the muscle fiber recruitment pattern related to the occurrence of $\dot{V}O_{2SC}$ using a previously employed exercise model for maintaining a given pedal rate throughout exercise and also using a newly designed exercise model for switching from low to high or from high to low pedal rates at the halfway point during constant- metabolic demand cycling exercise. We hypothesized that this newly designed exercise model could induce the different recruitment of muscle fibers between the first phase (~3 min) and the later phase (3 min~) of exercise. Consequently, the amplitude of the $\dot{V}O_{2SC}$ induced by switching pedal rates model should be different from that of the $\dot{V}O_{2SC}$ in the previously designed exercise model.

Materials and Methods

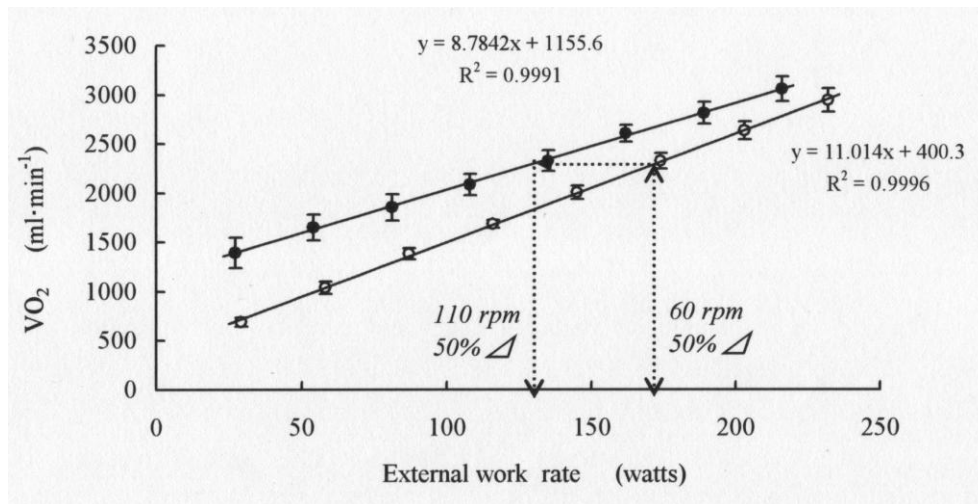
Subjects: Seven healthy male volunteers [mean \pm SD: age; 24 \pm 2 years, height 170 \pm 4 cm, body mass 64.8 \pm 7.5 kg] participated in this study. The exercise protocol and all risks and benefits associated with participation in the study were explained to each subject. All subjects gave their written informed consent prior to participating in this study. The experimental protocol used in this study was approved by the Ethics Committee for Human Subjects of the Kyushu Institute of Technology.

Protocol: All exercise tests were carried out on a mechanical braked-cycle ergometer (Monark 818E, Crescent AB, Varburg, Sweden). The subjects first performed two incremental exercise tests at pedal rates of 60 rpm and 110 rpm to determine their ventilatory threshold (VT; decisions of VT was described later) and peak oxygen uptake ($\dot{V}O_{2peak}$) at each pedal rate. Subsequently, they completed four square-wave transitions, two 6 min constant-load exercises and two 6 min constant-metabolic demand exercises with switching pedal rate at halfway point.

Incremental tests: Both pedal rates incremental exercise tests were carried out on a separate day and in a random order. The exercise test consisted of 4 min of unloaded pedaling followed by an increased work rate of 30 W (60 rpm) or 27.5 W (110 rpm) every 1 min until they could no longer maintain the requested pedal rate, despite verbal encouragement. The pulmonary gas exchange parameters were measured breath-by-breath (see below). The highest $\dot{V}O_2$ average over a 30 s interval was taken as the $\dot{V}O_{2peak}$. The estimated VT was determined as the breakpoint in the plot of CO_2 output as a function of $\dot{V}O_2$ (V-slope method)[6].

Square-wave transitions: The external work rates for four square-wave transitions were set at equal to $\dot{V}O_2$ at VT plus $\dot{V}O_2$ of 50% of the difference between VT and the $\dot{V}O_{2peak}$ for each pedal rate (50% Δ). Firstly, an external work



**Fig. 1**

Relationship between the oxygen uptake and the external work rate during incremental exercise with two different pedaling rates (○; 60 rpm, ●; 110 rpm)

rate corresponding to 50%Δ at 60 rpm was determined by interpolating the linear regression between the work rate and VO₂. Subsequently, VO₂ corresponding to 50%Δ at 60 rpm was interpolated to the linear regression between the work rate and VO₂ at 110 rpm during the incremental exercise test and the external work rate corresponding to 50%Δ at 110 rpm was thus determined (Fig. 1). Secondly, the subjects completed two square-wave transitions consisting of 2 min of unloaded pedaling followed by a transition to 6 min constant-load exercise requiring 50%Δ at 60 rpm (60con) and 110 rpm (110con) as control transition model. Each cycling test was completed on a separate day and the order of these tests was randomized. Finally, each subject completed additional two square-wave transitions to 6 min constant-metabolic demand exercise with switching pedal rates at the 3rd min of exercise as main transition model. The one square-wave transition test consisted of 2 min of unloaded pedaling followed by transition exercise requiring 50%Δ at 60 rpm for the first 3 min and then further requiring 50%Δ at 110 rpm for the later 3 min (60→110swi). The other square-wave transition test consisted of 2 min of unloaded pedaling followed by reverse order pedal rates (110→60swi). Because the total work rate (external plus internal work rates) was necessary to be remained constant throughout the exercise in the switching pedal

rate model (see data analysis for more detail of internal work rate), external work rate concomitant with the switched pedal rate was changed at the halfway point during exercise. Namely, when the pedal rate was switched from 60 to 110 rpm (60→110swi), external work rate was decreased. Inversely, in the switching pedal rate exercise of 110→60swi, external work rate was increased. The order of these tests was randomized. A schematic drawing of the four transitions tests is shown in Fig. 2.

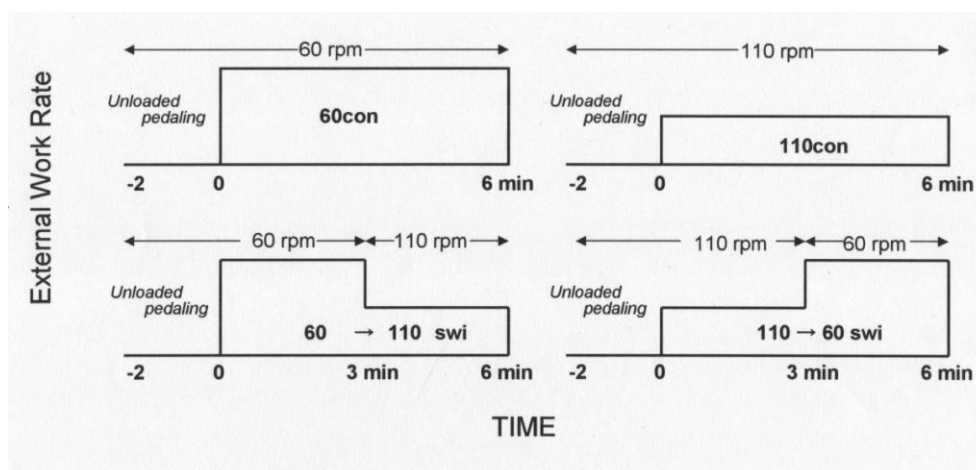


Fig. 2

Schematic illustrations of the square-wave transition exercise tests

In this study, because the main purpose was to compare the effect of two different exercise models on $\text{VO}_{2\text{SC}}$, the subjects performed only once of each square-wave transition test.

Measurement: The pulmonary gas exchange parameters were measured breath-by-breath using a metabolic measurement system (A-E 300S, Minato Medical Science Ins., Japan) during all exercise sessions. Minute ventilation (\dot{V}_E), VO_2 and carbon dioxide output (VCO_2) were continuously determined throughout the exercise tests and the data was stored on a hard disk for future analyses. The inspired and expired gas volumes were measured by a hot-wire flowmeter and the fractions of O_2 and CO_2 were measured by a paramagnetic oxygen analyzer and an infrared absorption analyzer, respectively. The flowmeter was calibrated before the exercise test by manually pumping a 2-liter syringe. The analyzers for O_2 and CO_2 were calibrated using gases of known concentrations before each exercise test.

Pulmonary gas exchange parameters were averaged across 30 s intervals. Fingertip capillary blood samples were taken before and immediately after the four transition-exercise tests to determine the whole blood lactate concentration ([La]). The samples were analyzed by a semi-automated lactate analyzer (YSI1500 Sport, Yellow Springs Ins., Ohio, USA), which was calibrated prior to the test sessions using a 5 mmol/l lactate standard solution provided by the manufacturer. The blood lactate accumulation (Δ [La]) was calculated as the difference between [La] at a resting state and immediately after exercise. The heart rate was measured telemetrically and recorded every 5 s during all exercise tests using a Polar S610i heart rate monitor (Polar Electro Oy, Finland).

The surface electromyogram (EMG) signal was obtained from the vastus lateralis using a differential surface electrode (DE-2.1, Bagnoli-4 EMG System, Delsys Inc., Boston, MA, USA) during four transition-exercise tests. The electrode contacts were made from 99.9% pure silver bars measuring 10 mm in length, 1 mm in diameter and spaced 10 mm apart for optimal frequency capture. The electrode placement for the vastus lateralis was the midpoint between the head of the greater trochanter and the lateral femoral epicondyle [21]. Before placing the electrode, the skin area was shaved and cleaned with ethyl alcohol. To facilitate further recording from the same placement during subsequent visits, the area of electrode placement was marked on the skin surface. To obtain accurate pedal rates during cycling, a hall-IC sensor detected the magnetic signals from a small, thin magnetic (1.8×2.0 cm) attached to the flywheel. The signals from EMG and the hall-IC sensor were simultaneously recorded at a sampling rate of 1000 Hz via an analog-to-digital (A/D) converter (PowerLab/8s, ADInstruments, Castle Hill, Australia) onto a computer hard drive.

Data analysis: The major concern in this study is to detect the amplitude of $\dot{V}O_{2SC}$ and it is unclear whether fitting higher order model for analysis of the $\dot{V}O_2$ kinetics would be appropriate for the newly exercise model with switching pedal rate at halfway point employed in this study. Generally, $\dot{V}O_{2SC}$ is defined as the difference between end-exercise $\dot{V}O_2$ and the steady state $\dot{V}O_2$ of phase II during exercise. In case of analysis without nonlinear exponential model, it is usually calculated as the difference between the $\dot{V}O_2$ at 3rd min during exercise and end-exercise $\dot{V}O_2$. However, a number of previous studies [4,7,20,25] show that the time delay for $\dot{V}O_{2SC}$ (in other word, onset of $\dot{V}O_{2SC}$; TDs) would be around 2nd min during transition exercise. Similarly, $\dot{V}O_2$ kinetics analyses using a nonlinear exponential model with respect to control transition exercise in this study provided TDs as 144±33 s (60con) and 127±30 s (110con), respectively (the results were not described in this paper). Therefore, the $\dot{V}O_{2SC}$ was calculated as the difference



between the $\dot{V}O_2$ at 2nd min of exercise and end-exercise (i.e. 6th min) $\dot{V}O_2$ in control and main transitions.

The flywheel frequency obtained from the signals of the hall-IC sensor was converted into pedal rates using the ratio of pedal to flywheel (i.e. 3.64). The total mechanical power output (W_{tot}) was calculated as the sum of the external power output delivered to the cycle ergometer and the estimated 'internal' power output. The internal power output refers to power output that is performed to overcome gravitational and inertial forces related to the movement of the exercising muscle. Therefore, the internal power output during cycling exercise has been reported to change dependent on the pedal rates [19]. The internal power outputs (W/kg) in this study was estimated as $0.153 \times \text{pedal rate}^3$, where pedal rate is in Hz, according to Minetti *et al.* [19]. Ferguson *et al.* [13] estimated the internal work during cycling exercise at different pedal rates by using the same method. A value of $\dot{V}O_2$ above a resting level ($\Delta\dot{V}O_2$) per unit of all work rate accomplished by the exercising muscle itself ($\Delta\dot{V}O_2/W_{tot}$) was used as an index of the oxygen cost for the newly designed exercise model in this study.

The raw EMG signals were passed through a 20-500 Hz band pass filter. For each burst of muscle activity, integrals of the EMG signal (iEMG) were determined every 30 s for each subject. The iEMG was normalized at the first 1 min-exercise value, which was assigned a value of 100%.

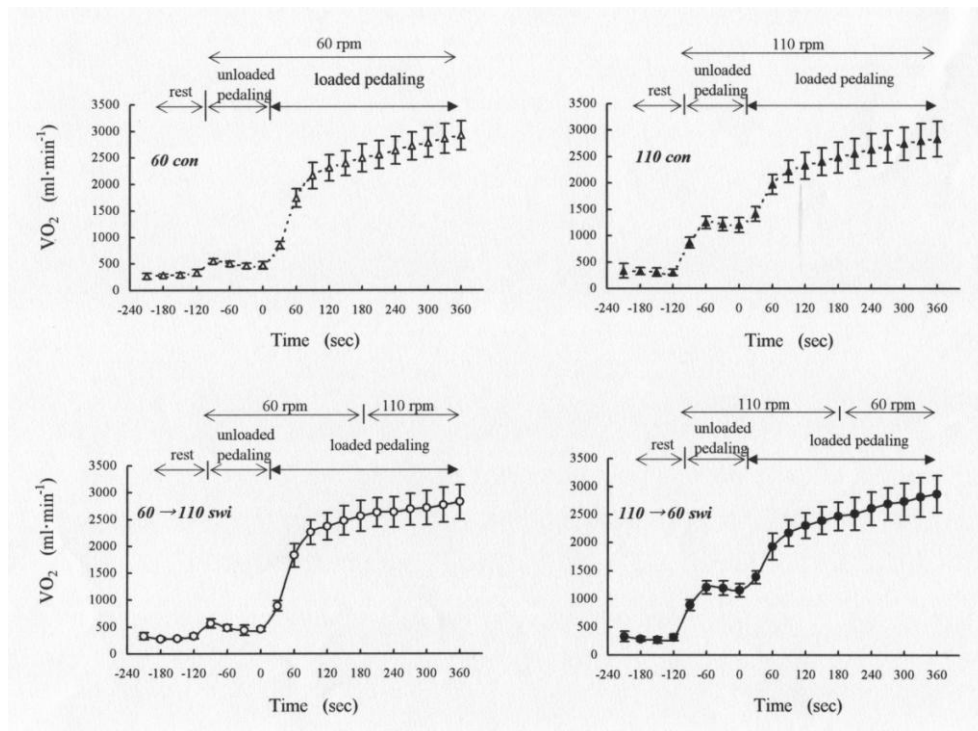
Statistical analysis: All data are presented as mean \pm SD. Comparisons between the responses at different square-wave transition exercises were made using one-way repeated-measure ANOVA design. The values of the iEMG were analyzed by two-way (exercise \times time) repeated-measures ANOVA design. When a significant effect was observed, such differences were analyzed using the Scheffe post hoc analysis. Statistical significance was accepted at $p < 0.05$.

Results

Incremental exercise test: The mean values for the $\dot{V}O_{2peak}$ and $\dot{V}O_2$ corresponding to VT ($\dot{V}O_2@VT$) were 2998 ± 303 and 1955 ± 221 ml/min for 60 rpm and 3055 ± 276 and 2101 ± 254 ml/min for 110 rpm, respectively. The differences of the $\dot{V}O_{2peak}$ and $\dot{V}O_2@VT$ between 60 and 110 rpm were small, but significant ($p < 0.05$), whereas the relative value of $\dot{V}O_2@VT$ to $\dot{V}O_{2peak}$ was not significantly different between both incremental exercises [65.3 ± 6.2 % at 60 rpm vs. 68.7 ± 4.5 % at 110 rpm, respectively].

Square-wave transitions: The mean responses of $\dot{V}O_2$ in four transitions are presented in Fig. 3.



**Fig. 3**

Oxygen uptake ($\dot{V}O_2$) responses to four square-wave transition exercises

1) Maintaining a given pedal rate throughout the exercise tests

The $\dot{V}O_2$ amplitude of unloaded pedaling exercise in 110con was significantly greater than that in 60con (Table 1). However, in the both pedal exercises, there was no difference in the $\dot{V}O_{2SC}$, measured as the difference between at the 2nd and end exercise $\dot{V}O_2$ (Table 1). The value of $\Delta\dot{V}O_2/W_{tot}$ at the later phase of exercise was greater in 60con than in 110con ($p < 0.05$, Fig. 5). The iEMG responses in both pedal rates were essentially unchanged until the end of exercise (Fig. 6). There was no significant difference in $\Delta[La]$ between 60con and 110con (Table 1).

2) Switching pedal rate at the halfway point of the exercise tests

Although the amplitude of $\dot{V}O_2$ during unloaded pedal exercise in 110→60swi was significantly greater than that in 60→110swi, there was no difference in $\dot{V}O_{2SC}$ between 60→110swi and 110→60swi as well as ΔLa [6.50 ± 1.05 mM for

60→110swi, and 6.78 ± 1.46 mM for 110→60swi] (Table 1). Fig. 4 shows the external, internal and total power outputs during the exercise tests. The external power output was greater at the phase of 60 rpm than at the phase of 110 rpm. On the other hand, the internal power output was greater at the phase of 110 rpm than at the phase of 60 rpm. As a result, the total power outputs were similar levels in both phases. Despite the fact that $\dot{V}O_2$ and W_{tot} during main exercises model in 60→110swi and 110→60swi maintained almost the same levels throughout the exercise tests (Figs. 3 and 4), $\Delta\dot{V}O_2/W_{tot}$ decreased after switching pedal rate in 60→110swi and increased after the switching pedal rate in 110→60swi (Fig. 5). Similarly, the iEMG responses during exercises tended to decrease (60→110swi) or increase (110→60swi) after switching pedal rates at the halfway point of exercise as shown in Fig. 6. Furthermore, it was found in both 60→110swi and 110→60swi that the changes in $\Delta\dot{V}O_2/W_{tot}$ after switching pedal rates occurred concomitant with the changes in iEMG.

Table 1

$\dot{V}O_2$ and blood lactate responses to four square-wave transitions. $\Delta(\text{end-2nd min})$; the difference in $\dot{V}O_2$ between at end exercise and 2nd min during main exercise, which was calculated as $\dot{V}O_{2SC}$ in this study, % $\dot{V}O_{2SC}$; relative contribution of the $\dot{V}O_{2SC}$ to a net increase in $\dot{V}O_2$ at end exercise, $\Delta[\text{La}]$; blood lactate accumulation

		60con	110con	60→110swi	110→60swi
$\dot{V}O_2$					
at rest	(ml·min ⁻¹)	295±37	320±75	305±33	300±48
at 0 min	(ml·min ⁻¹)	469±69	1202±142*	457±37	1154±118*
at 2nd min	(ml·min ⁻¹)	2314±247	2324±253	2366±253	2303±225
end exercise	(ml·min ⁻¹)	2917±275	2831±332	2822±321	2870±331
$\Delta(\text{end-2nd min})$	(ml·min ⁻¹)	604±120	506±169	457±133	567±123
% $\dot{V}O_{2SC}$	(%)	23±4	20±5	18±5	22±2
$\Delta[\text{La}]$	(mM)	7.26±1.15	6.0±1.6	6.50±1.05	6.78±1.48

*; vs. 60con and 60→110swi (p<0.05)



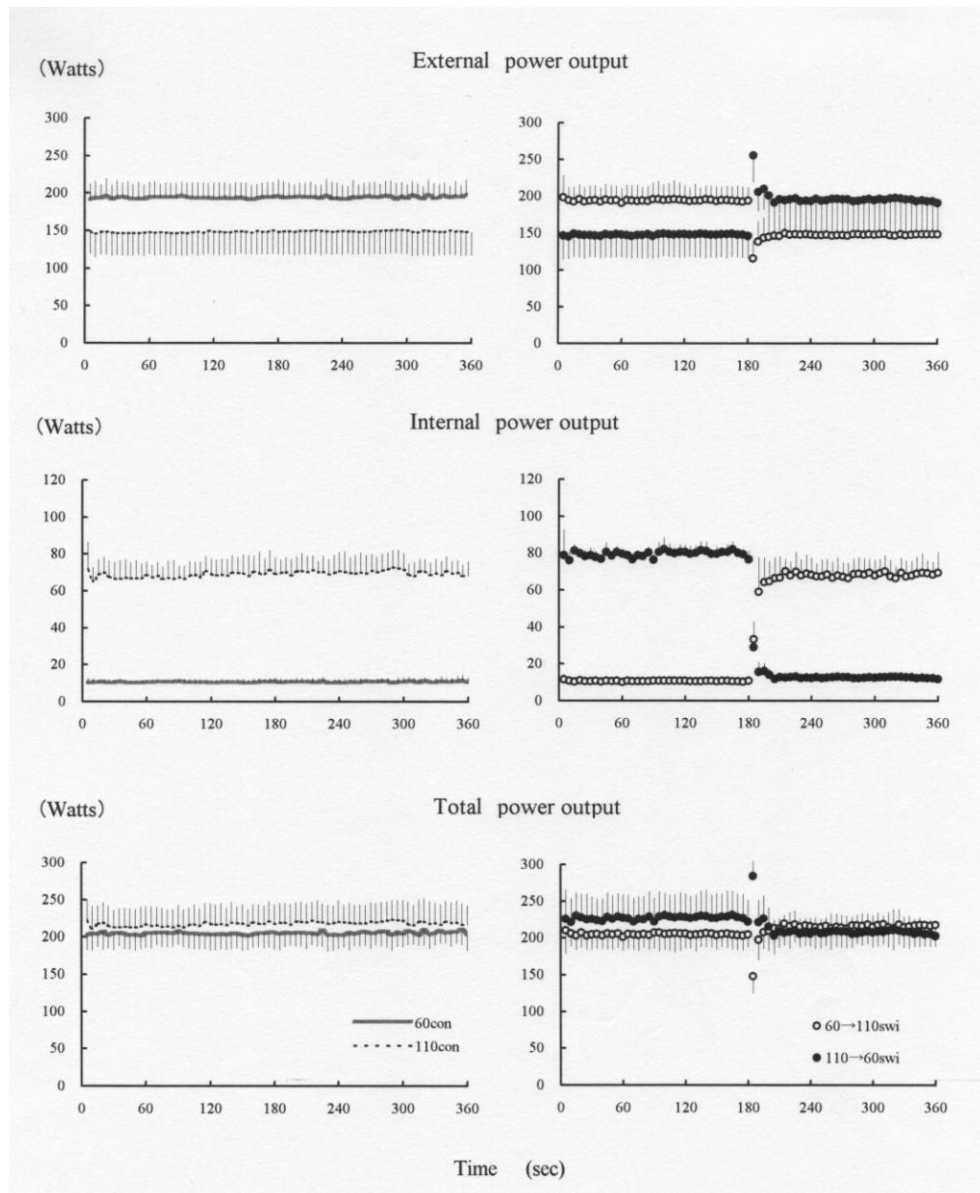
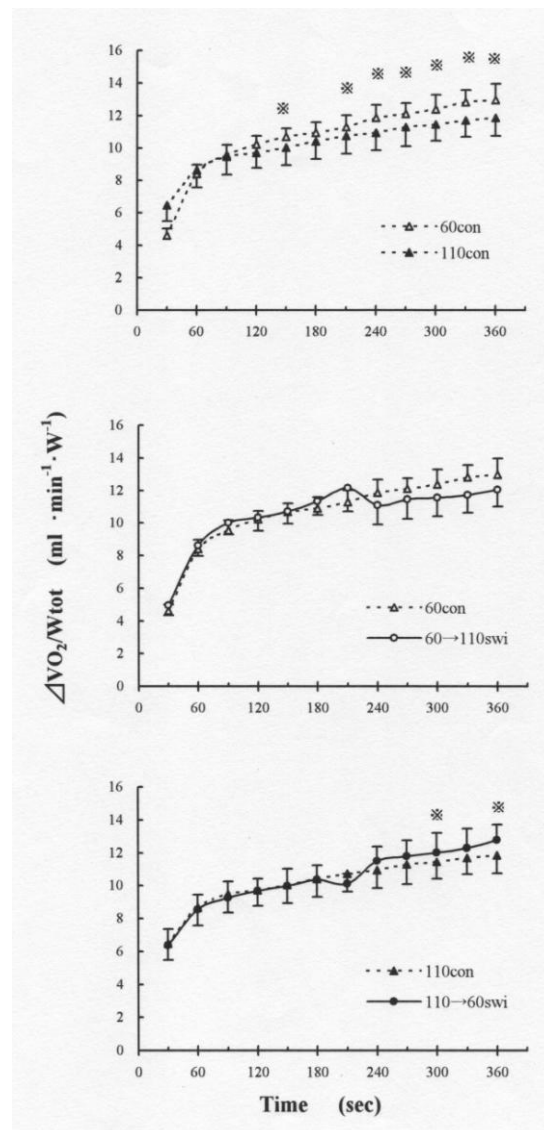


Fig. 4
The external, internal and total power outputs during square-wave transition exercises. Left; 60con and 110con, right; 60→110swi and 110→60swi



**Fig. 5**

The mean oxygen cost response to square-wave transition exercises. The oxygen cost was expressed as VO_2 above rest / total power output ($\Delta\text{VO}_2/W_{\text{tot}}$)

*indicated significant differences among the square-wave transitions at each time point



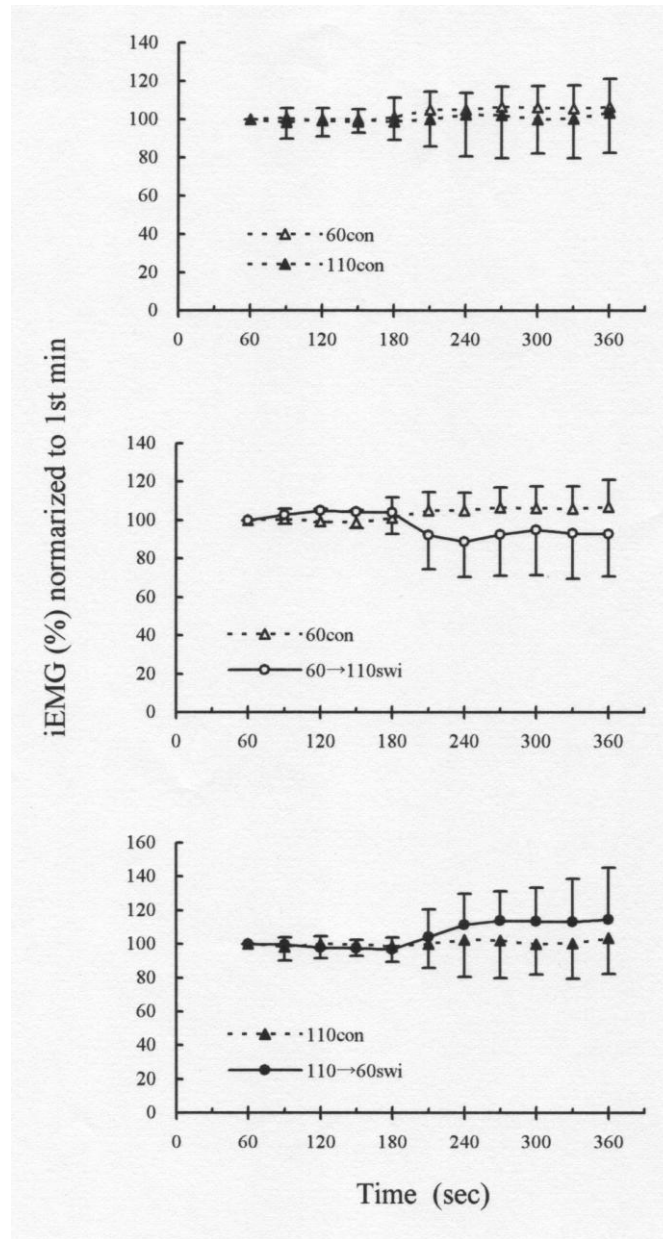


Fig. 6
Integrated electromyogram (iEMG) response to square-wave transition exercises



Discussion

It has been generally considered that a large part of $\dot{V}O_{2SC}$ is likely attributable to the mechanical or metabolic changes in the exercising limbs, and a possible explanation for this would be the change in the fiber type recruitment patterns [4,7,18,25,26]. An exercise model for different pedal rate cycling has been used as a useful tool for examining the mechanical and metabolic changes within the exercising muscle [14,16-19]. Barstow *et al.* [4] compared the amplitudes of $\dot{V}O_{2SC}$ among the different pedal rates (45~90 rpm) at the same metabolic demand cycling exercises, and reported no effect of pedal rate on the amplitude of $\dot{V}O_{2SC}$. Pringle *et al.* [25] indicated that the range of pedal rates employed was too narrow to change in the fiber type recruitment patterns, and investigated the effect of a wide range of pedal rates (35, 75, 115 rpm) on the amplitude of $\dot{V}O_{2SC}$ during constant-load exercise at the same metabolic demand. They have showed greater $\dot{V}O_{2SC}$ in exercise at 115 rpm compared with 35 rpm and 75 rpm, suggesting that the highest pedal rate would induce the recruitment of type II muscle fibers from the onset of exercise and recruited fatigue-sensitive type II muscle fibers related with the greater $\dot{V}O_{2SC}$ in exercise at 115 rpm. However, this notion seems likely to be questionable for understanding of the cause and effect of $\dot{V}O_{2SC}$. Because the different pedal rates exercises employed by Pringle *et al.* [25] were performed at the same metabolic demand, external work rate in highest pedal rate was lower level compared with the lowest pedal rate exercise. Similarly, the exercise tension in the exercising muscle would be lower level in the highest pedal rate. Taking into account that recruitment patterns of muscle fibers depend on not only contraction velocity but also developed tension [15], it would be raised whether the highest pedal rate cycling recruited more type II muscle fibers compared with the lowest pedal rate. Furthermore, it should be clarified whether or not a change in muscle fiber recruitments occurred at the later phase of exercise. No consensus on second matter has yet been reached from the exercise models used in previous studies. Therefore, it seems difficult to prove whether a change of muscle fiber recruitment pattern induces the $\dot{V}O_{2SC}$ based on the above mentioned exercise models. It is therefore necessary to examine the cause and effect relationship between the muscle fiber recruitment patterns and $\dot{V}O_{2SC}$ using an exercise model different from that used in previous studies. To our knowledge, this is the first study to examine the inducing factor(s) of the $\dot{V}O_{2SC}$ using a newly designed exercise model for switching the pedal rate at the halfway point of a cycling exercise.

Muscular fiber recruitment and the changes in $\Delta\dot{V}O_2/W_{tot}$: It has recently been demonstrated that the quantification of the total power output estimated as the sum



of the internal and external power outputs allows us to accurately evaluate the physiological responses during exercise [11]. Especially, the total work accomplished in the exercise model developed in this study must be evaluated, since the internal work varies dependent on the pedal rates [19] during cycling ergometry. Then, the value of $\Delta\text{VO}_2/\text{W}_{\text{tot}}$ estimated in this study would reflect the true oxygen cost per unit of all work accomplished by the exercising muscle itself. The exercise model for switching pedal rate at the halfway point of a cycling exercise regimen showed the $\Delta\text{VO}_2/\text{W}_{\text{tot}}$ to decrease from the phase of 60 rpm to the phase of 110 rpm while it inversely increased from the phase of 110 rpm to the phase of 60 rpm. The oxygen cost associated with the accomplished work might thus be expected to vary depending on the contribution of type I and type II fibers to the force production, and such fiber type recruitment patterns are thus considered to depend on not only the contraction velocity but also the developed tension in the exercising muscle. Ahlquist *et al.* [2] showed the glycogen depletion rate during the same metabolic cycling exercise regimen to be greater at 50 rpm (low velocity-high force) than at 100 rpm (high velocity-low force), thus indicating the greater recruitment of type II muscle fibers under a highly developed tension level (low velocity). We have considered as a physiological basis that more type II fibers would be recruited at a higher force production (i.e. higher external work) according to the size principle [15], even at a lower pedal rate. Therefore, the changes in $\Delta\text{VO}_2/\text{W}_{\text{tot}}$ obtained in this study suggest that switching pedal rate from 110 to 60 rpm during cycling exercise induced a shift to a greater recruitment of type II muscle fibers, while switching pedal rate from 60 to 110 rpm induced a shift to a less recruitment of type II muscle fibers. As a result, the increased or decreased recruitment proportion of low-efficiency type II muscle fibers are considered to cause higher or lower values in $\Delta\text{VO}_2/\text{W}_{\text{tot}}$ due to the exercise model for switching pedal rate at the halfway point of cycling exercise, which is consistent with the notion that the greater contribution of type II fibers to force production thereby results in to a higher oxygen cost or a steeper $\Delta\text{VO}_2/\Delta\text{WR}$ slope during cycling exercise [16,22,28].

Muscular fiber recruitment and the changes in iEMG: In the present study, the relative iEMG due to switching pedal rate at the halfway point of cycling exercise revealed a tendency to change accompanied by a response of the $\Delta\text{VO}_2/\text{W}_{\text{tot}}$ (Figs. 5 and 6). In this study, because the vastus lateralis is mainly recruited during cycling exercise, EMG data was obtained from the only vastus lateralis. However, a multi-joint exercise such as cycling is requiring the involvement of several muscle groups, and then the simultaneous EMG measurement for all of the major muscle groups would be needed to clarify the accurate activity level in exercising



muscle [8]. Furthermore, measure of surface EMG may not be sufficiently sensitive to detect the subtle changes in motor unit recruitment during dynamic exercise. Therefore, the results of EMG in this study might be also interpreted carefully, with a caution of the limitations to the methods as described by Jones *et al.* [17]. However, if it is postulated that a change in the relative iEMG during exercise represents a change in the motor units (MUs) recruitment and/or MU firing rate [24,26], the exercise model for switching pedal rate at the halfway point of cycling exercise in this study is considered to induce a change in the muscle fiber recruitment pattern and/or a change in the recruited number of muscle fibers.

Possible factors causing the $\dot{V}O_{2SC}$: From the results of $\Delta\dot{V}O_2/W_{tot}$ and relative iEMG in this study, the exercise model for switching pedal rate might be considered to induce the different muscle fiber recruitment patterns at the later phase of exercises compared with the control exercise model. However, there were no differences in the amplitudes of $\dot{V}O_{2SC}$ among the four trials (i.e. 60con, 110con, 60→110swi, 110→60swi). These results would imply that a change in the muscle fiber recruitment pattern was not associated directly with the factor(s) inducing $\dot{V}O_{2SC}$ during the same metabolic demand cycling exercise regimen. Then another explanation for the occurrence of $\dot{V}O_{2SC}$ should be considered, which is directly connected with the factor(s) originating from the exercising muscle. A greater accumulation of [La] was observed as a result of the exercise tests, but there were no differences in Δ [La] between the previously used and newly designed exercise models. The fatigue-induced accumulation of metabolites (i.e. H^+ , $H_2PO_4^-$, lactate $^-$) or a depletion of the high-energy phosphate pool may impair the ATPase activity connected with Ca^{2+} reaccumulation into the sarcoplasmic reticulum [1,3,14]. Therefore, a progressive increase in the ATP requirement associated with non-force generating processes (ex. Ca^{2+} pumping, Na^+/K^+ pumping) during exercise may be indicated as one of the possible factors causing $\dot{V}O_{2SC}$. Moreover, another possibility is that the increased total energy turnover, which results from a reduction in the amount of free energy released from the splitting of ATP, may induce a greater ATP requirement during the same metabolic exercise regimen [3,10]. It would be speculated that progressive increases in metabolites like ADP and Pi, as well as the lowering of pH levels and the depletion of the high-energy phosphate pool during heavy exercise, may be related to a lowering of free energy in ATP hydrolysis. Taken together, we have considered that the nature of the initially-recruited fibers, rather than sequential changes in recruitment over time, might be the key. Further studies are needed to verify the possibility of this consideration.



References

1. Abbate F., C.J. De Ruiter, C.Offringa, A.J.Sargeant, A. De Haan (2002) In situ rat fast skeletal muscle is more efficient at submaximal than at maximal activation levels. *J.Appl.Physiol.* 92:2089-2096
2. Ahlquist L.E., D.R.Bassett Jr., R.Sufit, F.J.Nagle, D.P.Thomas (1992) The effect of pedaling frequency on glycogen depletion rates in type I and type II quadriceps muscle fibers during submaximal cycling exercise. *Eur.J.Appl.Physiol.* 65:360-364
3. Bangsbo J., P.Krustrup, J.Gonzalez-Alonso, B.Saltin (2001) ATP production and efficiency of human skeletal muscle during intense exercise: effect of previous exercise. *Am.J.Physiol.Endocrinol.Metab.* 280:E956-E964
4. Barstow T.J., A.M.Jones, P.H.Nguyen, R.Casaburi (1996) Influence of muscle fiber type and pedal frequency on oxygen uptake kinetics of heavy exercise. *J.Appl.Physiol.* 81:1642-1650
5. Barstow T.J., A.M.Jones, P.H.Nguyen, R.Casaburi (2000) Influence of muscle fiber type and fitness on the oxygen uptake/power output slope during incremental exercise in humans. *Exp.Physiol.* 85:109-116
6. Beaver W.L., K.Wasserman, B.J.Whipp (1986) A new method for detecting anaerobic threshold by gas exchange. *J.Appl.Physiol.* 60:2020-2027
7. Borrani F., R.Candau, G.Y.Millet, S.Perrey, J.Fuchslocher, J.D.Rouillon (2001) Is the VO_2 slow component dependent on progressive recruitment of fast-twitch fibers in trained runners? *J.Appl.Physiol.* 90:2212-2220
8. Burnley M., J.H.Doust, D.Ball, A.M.Jones (2002) Effects of prior heavy exercise on VO_2 kinetics during heavy exercise are related to changes in muscle activity. *J.Appl.Physiol.* 93:167-174
9. Crow M.T., M.J.Kushmerick (1982) Chemical energetics of slow- and fast-twitch muscles of the mouse. *J.Gen.Physiol.* 79:147-166
10. diPrampo P.E., J.Piiper (2003) Effects of shortening velocity and of oxygen uptake consumption on efficiency of contraction in dog gastrocnemius. *Eur.J.Appl.Physiol.* 90:270-274
11. Ferguson R.A., P.Aagaard, D.Ball, A.J.Sargeant, J.Bangsbo (2000) Total power output generated during dynamic knee extensor exercise at different contraction frequencies. *J.Appl.Physiol.* 89:1912-1918
12. Ferguson R.A., D.Ball, P.Krustrup, P.Aagaard, M.Kjaer, A.J.Sargeant, Y.Hellsten, J.Bangsbo (2001) Muscle oxygen uptake and energy turnover during dynamic exercise at different contraction frequencies in humans. *J.Physiol.* 536:261-271
13. Ferguson R.A., D.Ball, A.J.Sargeant (2002) Effect of muscle temperature on rate of oxygen uptake during exercise in humans at different contraction frequencies. *J.Exp.Biol.* 205:981-987
14. Gaesser G.A., D.C.Poole (1996) The slow component of oxygen uptake kinetics in humans. *Exerc.Sports Sci.Rev.* 24:35-70



15. Henneman E., H.P.Clamann, J.D.Gillies, R.D.Skinner (1974) Rank order of motoneurons within a pool: law of combination. *J.Neurophysiol.* 37:1338-1349
16. Jones A.M., I.T.Campbell, J.S.M.Pringle (2004) Influence of muscle fiber type and pedal rate on the $\dot{V}O_2$ -work rate slope during ramp exercise. *Eur.J.Appl.Physiol.* 91:238-245
17. Jones A.M., J.S.M.Pringle, H.Carter (2005) Influence of muscle fibre type and motor unit recruitment on $\dot{V}O_2$ kinetics. In: A.M. Jones and D.C. Poole (eds.) Oxygen uptake kinetics in sport, exercise and medicine. Routledge, London, pp 261-293
18. Krstrup P., K.Soderlund, M.Mohr, J.Bangsbo (2004) Slow-twitch fiber glycogen depletion elevates moderate-exercise fast-twitch fiber activity and O_2 uptake. *Med.Sci.Sports Exerc.* 36:973-982
19. Minetti A.E., J.Pinkerton, P.Zamparo (2001) From bipedalism to bicyclism: evolution in energetics and biomechanics of historic bicycles. *Proc.R.Soc.Lond.B.* 268:1351-1360
20. Perrey S., R.Candau, J.D.Rouillon, R.L.Hughson (2003) The effect of prolonged submaximal exercise on gas exchange kinetics and ventilation during heavy exercise in humans. *Eur.J.Appl.Physiol.* 89:587-594
21. Pincivero D.M., R.M.Campy, Y.Salfetonikov, A.Bright, A.J.Coelho (2001) Influence of contraction intensity, muscle, and gender of median frequency of the quadriceps femoris. *J.Appl.Physiol.* 90:804-810
22. Poole D.C., T.J.Barstow, G.A.Gaesser, W.T.Willis, B.J.Whipp (1994) $\dot{V}O_2$ slow component: physiological and functional significance. *Med.Sci.Sports Exerc.* 26:1354-1358
23. Poole D.C., W.Schaffartzik, D.R.Knight, T.Derion, B.Kennedy, H.J.Guy, R.Prediletto, P.D.Wagner (1991) Contribution of exercise legs to the slow component of oxygen uptake kinetics in humans. *J.Appl.Physiol.* 71:1245-1253
24. Pringle J.S.M., H.Carter, J.H.Doust, A.M.Jones (2002) Oxygen uptake kinetics during horizontal and uphill treadmill running in humans. *Eur.J.Appl.Physiol.* 88:163-169
25. Pringle J.S.M., J.H.Doust, H.Carter K.Tolfrey, A.M.Jones (2003) Effect of pedal rate on primary and slow-component oxygen uptake responses during heavy-cycle exercise. *J.Appl.Physiol.* 94:1501-1507
26. Shinohara M., T.Moritani (1992) Increase in neuromuscular activity and oxygen uptake during heavy exercise. *Ann.Physiol.Anthrop.* 11:257-262
27. Whipp B.J., K.Wasserman (1972) Oxygen uptake kinetics for various intensities of constant-load work. *J.Appl.Physiol.* 33:351-356
28. Willis W.T., M.R.Jackman (1994) Mitochondrial function during heavy exercise. *Med.Sci.Sports Exerc.* 26:1347-1354
29. Zolads J.A., A.C.H.J.Rademaker, A.J.Sargeant (2000) Human muscle power generating capability during cycling at different pedalling rates. *Exp.Physiol.* 85:117-124

