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Examination of Oxygen Uptake Kinetics in Decremental Load Exercise by a Numerical Computation Model

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Abstract The purpose of this study was to establish a numerical computation model for estimation of oxygen uptake ($\dot{V}O_2$) kinetics in decremental load exercise (DLE) starting from a work rate (WR) above the ventilatory threshold ($>VT$). In the model, WR in DLE were separated into several steps (constant load exercise, CLE) of which the durations increased step by step. $\dot{V}O_2$ kinetics in each step was estimated using an exponential equation, and the sum of $\dot{V}O_2$ values from all steps at a given time was regarded as simulated $\dot{V}O_2$ in DLE. In the model, the time constants were set symmetrically in a step $<VT$ and asymmetrically in a step $>VT$ at onset and offset (τ_{off}) of exercise. As a result, simulated $\dot{V}O_2$ qualitatively, but not quantitatively, approximated measured $\dot{V}O_2$. Consequently, we incorporated a new model in which a step $>VT$ was subdivided into several parts. Although there was a slight difference quantitatively, the interval of subdivision of 3.0 min and τ_{off} of 2.8 min allowed for qualitative approximation. The numerical computation model adopted in this study is useful for estimation of $\dot{V}O_2$ kinetics during DLE starting from high intensity ($>VT$). *J Physiol Anthropol* 27(5): 247–254, 2008
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Keywords: decremental-load exercise, oxygen uptake, simulation model

Introduction

Decremental load exercise (DLE) is a work mode in which work rate (WR, watts [W]) decreases from the onset until the end of exercise at a constant rate. There have been few studies using DLE in comparison with the number of studies using constant load exercise (CLE) or incremental load exercise (ILE). However, studies using DLE have recently been performed to examine the factors that determine oxygen

uptake ($\dot{V}O_2$) kinetics as have been examined in other work modes (Whipp et al., 1992; Horiuchi and Yano, 1994, 1997). Whipp et al. (1992) examined $\dot{V}O_2$ kinetics in DLE starting from maximal work load level, and they found that $\dot{V}O_2$ in DEL exponentially increased and decreased linearly until the end of the exercise. $\dot{V}O_2$ in DLE was compared with $\dot{V}O_2$ in ILE at the same WR, and it was found that the slope of the $\dot{V}O_2$ -WR relationship obtained in an area of the linear portion was higher than that in ILE ($14.3 \text{ ml} \cdot \text{min}^{-1}$ in DLE and $10.2 \text{ ml} \cdot \text{min}^{-1}$ in ILE). The difference in the slopes is thought to be related to repayment of a lactic acid oxygen debt (O_2 debt) because DLE was performed from a WR above the ventilatory threshold (VT) (Horiuchi and Yano, 1994). At the onset of DLE, lack of oxygen supply (oxygen deficit) occurs, and the deficit is repaid during DLE. This is known as O_2 debt.

Horiuchi and Yano (1997) examined the effect of prolonged exercise (PE) on $\dot{V}O_2$ during DLE. They assumed that when considerable energy is used during PE, the amount of lactate production will fall and consequently $\dot{V}O_2$ in DLE will decrease. The sum of $\dot{V}O_2$ from the onset to the end of DLE was significantly lower after PE than before PE, suggesting that $\dot{V}O_2$ in DLE includes repayment of lactic O_2 debt. However, Yano et al. (2004) reported that there was no significant differences in the slope of the $\dot{V}O_2$ -WR relationship obtained in a low-intensity area (below 50 W) of DLE regardless WR (120~240 W) at the onset of DLE. This result cannot be explained by the repayment of lactic O_2 debt because the repayment of lactic O_2 debt continues for a long time after the end of CLE. They therefore speculated that the steep slope of $\dot{V}O_2$ in DLE was correlated with excess $\dot{V}O_2$ but not with lactic O_2 debt.

Yano et al. (2003) proposed a simulation model for approximating $\dot{V}O_2$ in DLE and confirmed that the simulation model was valid for approximating $\dot{V}O_2$ in DLE starting from low-intensity exercise. This result indicates that $\dot{V}O_2$ in DLE starting from a WR not only above the VT but also below the VT includes O_2 debt. The amount of $\dot{V}O_2$ in DLE starting from

a WR above the VT contains superfluous oxygen (Yano et al., 2004). It is thought that the simulation model of Yano et al. (2003) cannot simply be applied to examine $\dot{V}O_2$ in DLE starting from a WR above the VT.

Thus, the purposes of this study were to establish a computation model for approximating $\dot{V}O_2$ in DLE starting from a WR above the VT and to examine the relationship between excess $\dot{V}O_2$ and O_2 debt in DLE starting from a WR above the VT.

Methods

Six healthy males participated in this study. The subjects' mean (\pm SD) age, height and body weight were 24 ± 3.1 years, 171 ± 5.7 cm, and 64 ± 5.6 kg, respectively. Informed consent was obtained after explaining the purpose of the experiment, the procedure and possible risks. The Ethics Committee of Hokkaido University Graduate School of Education approved the present study.

All exercise tests were performed using a computer-controlled bicycle ergometer (232CXL, Combi, Tokyo, Japan). In the first experiment, each subject performed ILE to determine the VT and $\dot{V}O_2$ peak. Each subject exercised on the ergometer for 4 min at 0 watts (unloaded cycling exercise) after a 5-min rest period. This was followed by ILE of 15 watts per min until the subject could no longer maintain a rotation rate of 60 rpm. On separate days, DLE tests with peak WR of 120 W (DLE₁₂₀) and 240 W (DLE₂₄₀) were performed. After cycling at a work rate of zero watts for 4 min, the work rate was suddenly increased to the target value, and then the work rate was reduced in ramp mode at a rate of $15 \text{ watts} \cdot \text{min}^{-1}$ until it reached zero watts.

$\dot{V}O_2$ and CO_2 output ($\dot{V}CO_2$) were measured breath-by-breath using a respiratory gas analyzer (AE-280S, Minato Medical Science, Osaka, Japan). The flow volumes of inspiration and expiration were determined using a hot-wire respiratory flowmeter. The flow signals were electrically integrated for each breath and converted to ventilation per minute. The respiratory flow meter was calibrated using a 2-liter syringe. The O_2 and CO_2 concentrations were analyzed using a zirconium sensor and infrared absorption analyzer, respectively. $\dot{V}O_2$ and $\dot{V}CO_2$ data were output every 15 seconds.

The VT of each subject was determined by the V-slope method (Beaver et al., 1986) using data obtained in the ILE test. $\dot{V}O_2$ was plotted against $\dot{V}CO_2$. Two regression lines were drawn, one at the low-power output phase and one at the high-power output phase. The intercept of the two regression lines was defined as VT. $\dot{V}O_2$ peak was taken as the highest 15-s average achieved during the ILE test.

$\dot{V}O_2$ in the DLE test was plotted against WR and then two regression lines ($\dot{V}O_2$ slope) were drawn, one at the low-power output phase and one at the high-power output phase, according to the method of Yano et al. (2004). The slopes between $\dot{V}O_2$ and WR were determined within the low-power

output phase (below 50 W) in DLE₁₂₀ and DLE₂₄₀ and within the high power output phase (100–150 W) in DLE₂₄₀.

Description of the model

WR and exercise durations used in a numerical computation model were equivalent to those in the actual experiment design. As shown in Fig. 1, WR of 240 W in the DLE test was divided into 64 CLEs of which the durations increase step by step. Therefore, the work rate of each step was $3.75 (=240/64)$ watts. The exercise duration (D_1) of the first step ($S=1$) in the 64 steps was $0.25 (=16/64)$ min, and the duration increased by 0.25 min in each step (D_n) (for example, $D_1=0.25$ min, $D_2=0.50$ min, $D_3=0.75$ min, ..., $D_n=0.25 \times n$ min).

$\dot{V}O_2$ for one watt ($\dot{V}O_2$ slope; gain) in the numerical computation model was assumed to increase by

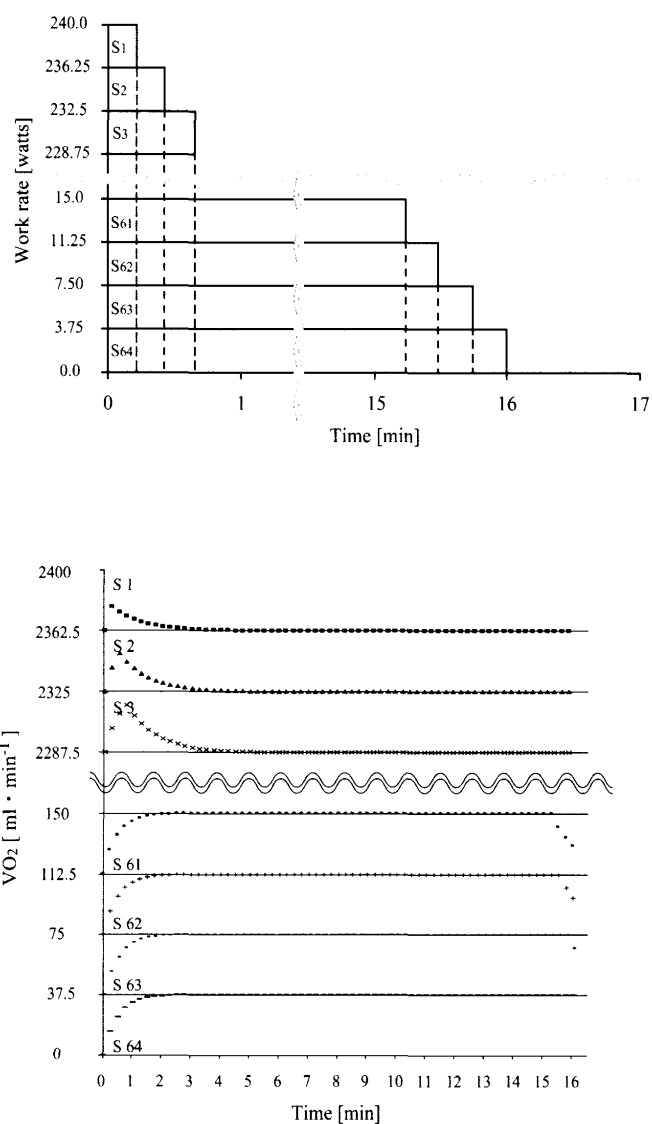


Fig. 1 The upper panel shows the work rate in decremental load exercise (DLE) starting from 240 W with a decreasing rate of 15 W. There are 64 steps. These steps are divided into each constant load exercise (CLE). Each CLE finishes step by step from the top to the bottom. The lower panel shows the kinetics of oxygen uptake ($\dot{V}O_2$) in each step. $\dot{V}O_2$ increases at the onset of each step and decreases at the offset of each step. Each step corresponds to each step in upper panel.

$10 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$. Therefore, the amplitude of $\dot{V}O_2$ in each step (A_m) was $37.5 (=3.75 \times 10) \text{ ml} \cdot \text{min}^{-1}$. The time constant of onset of exercise (τ_{on}) was assumed to be 0.5 min (Özyener et al., 2001; Barstow et al., 1994). $\dot{V}O_2$ kinetics at the onset of exercise in each step (${}_E\dot{V}O_2(t)_n$) was estimated using the following equation (Yano et al., 2003).

$${}_E\dot{V}O_2(t)_n = A_m \times (1 - \exp(-t/\tau_{on})) \quad (1)$$

$$0 \leq t \leq D_n \quad (D_n = 0.25 \times n)$$

$$\text{If } t > D_n$$

$${}_E\dot{V}O_2(t)_n = 0.$$

Here, ${}_E\dot{V}O_2(t)$ is the value of oxygen uptake during exercise, n is the number of steps, A_m is the amplitude of $\dot{V}O_2$ in each step ($37.5 \text{ ml} \cdot \text{min}^{-1}$), τ_{on} is the time constant of the system at the onset of exercise ($\tau_{on} = 0.5 \text{ min}$), D_n is the exercise duration in each step, and t is time. The value of oxygen uptake during exercise was obtained by Eq (1). When a given time is more than the duration of some steps ($t > D_n$), the values of ${}_E\dot{V}O_2(t)$ in those steps become zero.

$\dot{V}O_2$ kinetics at the offset of exercise in each step (${}_R\dot{V}O_2(t)_n$) was estimated using the following equation (Yano et al., 2003).

$${}_R\dot{V}O_2(t)_n = B_n - B_n \times (1 - \exp(-(t - D_n)/\tau_{off})) \quad (2)$$

$$= B_n \times \exp(-(t - D_n)/\tau_{off})$$

$$D_n < t, \quad D_n = 0.25 \times n$$

$$\text{If } t < D_n$$

$${}_R\dot{V}O_2(t)_n = 0.$$

Here, ${}_R\dot{V}O_2(t)$ is the value of oxygen uptake during recovery, t is a given time, τ_{off} is the time constant of the system at the offset of exercise, and B_n is the value of ${}_E\dot{V}O_2(t)$ at the end of exercise in each step. τ_{off} was set to 0.5 min in each step below the VT, while τ_{off} was set to the value more than 0.5 min in each step above the VT. B_n is the value in Eq. (1) when time is equal to D_n ($t = D_n$).

That is,

$$B_n = A_m \times (1 - \exp(-D_n/\tau_{on})) = {}_E\dot{V}O_2(D_n) \quad (3)$$

Note that B_n is not always equal to A_m because B_n is a value at the end of exercise. When a given time is less than the duration of some steps ($t < D_n$), the values of ${}_R\dot{V}O_2(t)$ in those steps become zero. The sum of $\dot{V}O_2(t)$ values (both ${}_E\dot{V}O_2(t)$ and ${}_R\dot{V}O_2(t)$) in each step from step one (S_1) to step 64 (S_{64}) at a given time becomes net oxygen uptake (${}_N\dot{V}O_2$) in DLE.

That is,

$${}_N\dot{V}O_2 = \sum_1^{64} [{}_E\dot{V}O_2(t) + {}_R\dot{V}O_2(t)] \quad (4)$$

Subdivision model

As shown in Fig. 2, $\dot{V}O_2$ kinetics in each step above the VT was subdivided. In this model, $\dot{V}O_2$ kinetics was alternated at a

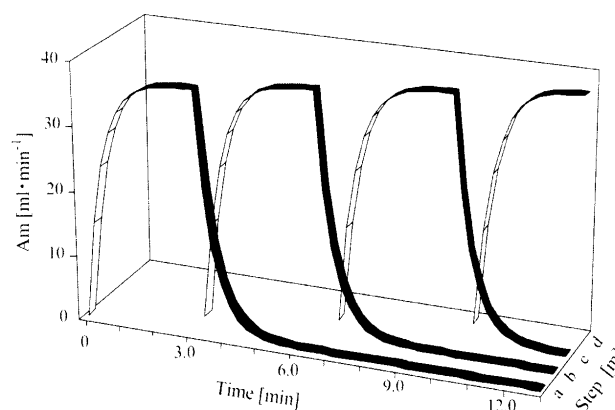


Fig. 2 Subdivision model. The panel shows the model in which the kinetics of oxygen uptake ($\dot{V}O_2$) was alternated at subdivision interval of 3.0 min in a single step. After onset of exercise, Step A will stop and change recovery phase at 3.0 min. Simultaneously, Step B becomes active phase.

Table 1 Parameter values used for the numerical computation model.

Time constant (τ)		Subdivision interval (RT)	Gain ($\dot{V}O_2 \cdot \text{W}^{-1}$)
Onset (τ_{on})	Offset (τ_{off})		
[min]		[min]	[$\text{ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$]
0.5	0.5–3.0	0.5–3.0	10

certain interval in a single step.

That is,

$${}_E\dot{V}O_2(t)_n = A_m \times (1 - \exp(-(t - TD)/\tau_{on})) \quad (5)$$

$$0 \leq t \leq D_n \quad (D_n = 0.25 \times n)$$

$$\text{If } RT < D_n$$

$$TD_1 = RT, \quad TD_2 = D_n - RT, \quad TD_3 = D_n - 2RT, \dots, \quad (\because TD_n \geq 0)$$

$${}_E\dot{V}O_2(t)_n = A_m \times (1 - \exp(-(t - TD)/\tau_{on})) + A_m \times (1 - \exp(-(t - (D_n - RT))/\tau_{on})) \quad (6)$$

$$\text{else, If } RT \geq D_n$$

$$TD_n = D_n$$

$$\text{If } t > D_n$$

$${}_E\dot{V}O_2(t)_n = 0$$

Here, RT is the interval of subdivision, TD_n is time delay as to RT. Eq. (6) is an equation showing $\dot{V}O_2$ kinetics during exercise in addition to interval of subdivision. The relation between $\dot{V}O_2$ of arbitrary time (t) and during the exercise and the recovery is the same as Eq. (1). The parameters used in the numerical computation model were presented in Table 1.

The square value (${}_D\dot{V}O_2(t)$) of difference of measured $\dot{V}O_2$ and estimated $\dot{V}O_2$ at a given time was calculated and sum of ${}_D\dot{V}O_2(t)$ values in the total exercise durations was calculated.

That is,

$${}_D\dot{V}O_2(t) = [\text{measured } {}_D\dot{V}O_2(t) - \text{estimated } {}_D\dot{V}O_2(t)]^2 \quad (7)$$

$${}_T\dot{V}O_2 = \sum_0^{16} [{}_D\dot{V}O_2(t)] \quad (8)$$

RT and τ_{off} showing a minimum value of ${}_T\dot{V}O_2$ were regarded as optimal values in the numerical computation model

Results

The mean power output at the VT was 167 ± 23 W. The characteristics of measured $\dot{V}O_2$ in DLE₁₂₀ and DLE₂₄₀ are shown in the upper panel in Fig. 3. $\dot{V}O_2$ kinetics in DLE₂₄₀ exponentially increased at the onset of exercise and decreased until the end of exercise. The slope of the $\dot{V}O_2$ -WR relationship in the DLE₂₄₀ was $14.77 \pm 1.1 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$ within the high-power output phase (100–150 W) and decreased to $10.61 \pm 0.6 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$ within the low-power output phase (below 50 W). The slope in DLE₁₂₀ was $10.57 \pm 0.6 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$ at the low-power output phase (below 50 W). This slope value was close to that obtained within the low-power output phase in DLE₂₄₀. Then the regression line of the $\dot{V}O_2$ -WR relationship below 50 W was extrapolated to a high-power output phase. The differences

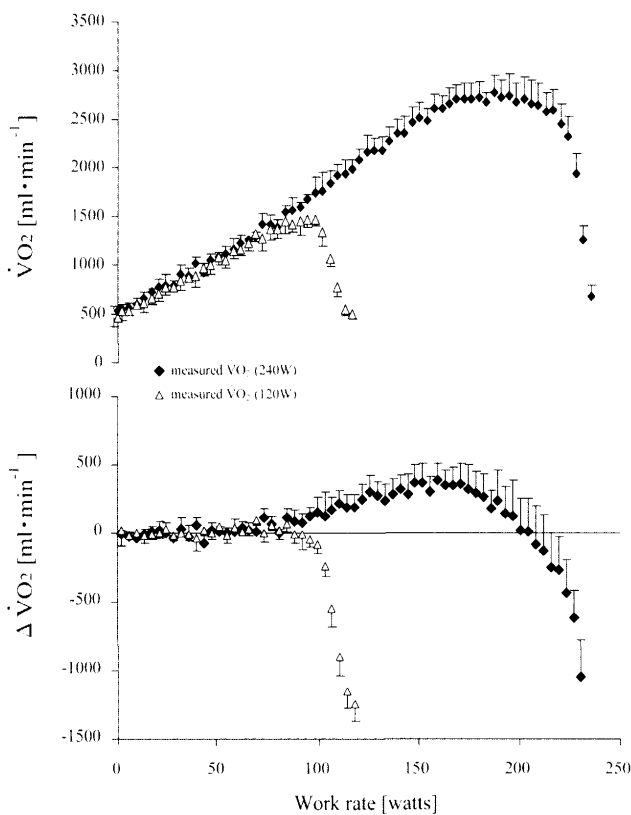


Fig. 3 Kinetics of oxygen uptake ($\dot{V}O_2$) during decremental load exercise (DLE). Comparison of $\dot{V}O_2$ in DLE starting from 240 W (\blacklozenge) with that in DLE starting from 120 W (\triangle) is shown in the upper panel. The lower panel shows a comparison of the difference ($\Delta\dot{V}O_2$) between measured $\dot{V}O_2$ and $\dot{V}O_2$ estimated from the work rate- $\dot{V}O_2$ relationship obtained below 50 W in DLE starting from 240 W (\blacklozenge) with that in DLE starting from 120 W (\triangle).

($\Delta\dot{V}O_2$) between measured $\dot{V}O_2$ and estimated $\dot{V}O_2$ were calculated and are shown in the lower panel in Fig. 3. $\Delta\dot{V}O_2$ in DLE₂₄₀ showed a negative value at the onset of exercise and shifted to a positive value in response to decrease in WR. The peak value of $\Delta\dot{V}O_2$ was about $500 \text{ ml} \cdot \text{min}^{-1}$. $\Delta\dot{V}O_2$ progressively decreased toward the zero $\text{ml} \cdot \text{min}^{-1}$ after reaching peak. Similarly, $\Delta\dot{V}O_2$ in DLE₁₂₀ showed a negative value at the onset of exercise. However there was no positive value in DLE₁₂₀.

$\dot{V}O_2$ values estimated by a numerical computation model in which time constants were the same at the onset and offset of each step (symmetry $\dot{V}O_2$ kinetics) and difference at the onset and offset of each step (asymmetry $\dot{V}O_2$ kinetics) are shown in Fig. 4. Measured $\dot{V}O_2$ values are also shown in the Fig. 4. The simulated $\dot{V}O_2$ and measured $\dot{V}O_2$ were the same at the onset of exercise. Measured $\dot{V}O_2$ values were higher than $\dot{V}O_2$ values estimated by a symmetrical model in a period from 200 to 100 W, and were lower than $\dot{V}O_2$ values estimated by an asymmetrical model in a period from 130 to 0 W. However, the values were the same below 100 W.

Figure 5 shows the effects of τ_{off} on $\dot{V}O_2$ kinetics in DLE. As described in Methods, τ_{on} was set to 0.5 min. $\dot{V}O_2$ kinetics during 2 min after the start of exercise were equivalent in all τ_{off} conditions. Therefore, $\dot{V}O_2$ and $\Delta\dot{V}O_2$ values increased with a rise in τ_{off} . However, even in a condition in which τ_{off} was set to 3.0 min, the $\Delta\dot{V}O_2$ was about one-half of the measured $\Delta\dot{V}O_2$ (Fig. 3). $\Delta\dot{V}O_2$ become positive with a decrease in exercise intensity, and showed a peak ($210 \text{ ml} \cdot \text{min}^{-1}$), and then decreased until the end of exercise. In a period below about 90 W, $\dot{V}O_2$ were similar in all τ_{off} conditions.

Figure 6 shows $\dot{V}O_2$ kinetics estimated by the numerical computation model in which the interval of subdivision (RT) is set to 0–3 min and both time constants (τ_{on} and τ_{off}) are fixed at 0.5 min. Estimated $\dot{V}O_2$ were the same in all RT conditions.

The upper panel in Fig. 7 shows $\dot{V}O_2$ kinetics estimated by the numerical computation model in which τ_{off} is fixed at 2.0 min and RT is set to 0–3.0 min. $\dot{V}O_2$ kinetics from 240 to

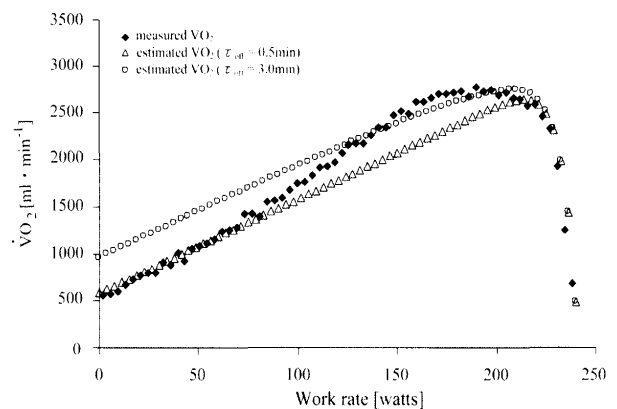


Fig. 4 Comparison of the oxygen uptake ($\dot{V}O_2$) simulated by numerical computation model in which time constants were the same at the onset and offset of each step (\triangle) and were set to 0.5 min at the onset and 3.0 min at the offset (\circ) and measured $\dot{V}O_2$ values (\blacklozenge).

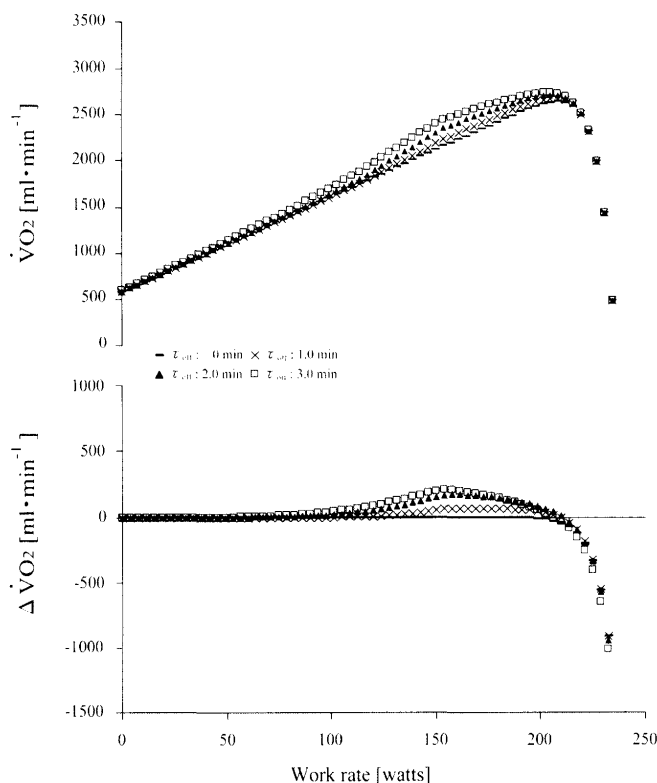


Fig. 5 Effects of time constant during recovery (τ_{off}) on oxygen uptake ($\dot{V}O_2$) in decremental load exercise (DLE). Time constant (τ_{on}) was set to 0.5 min. $\dot{V}O_2$ and $\Delta\dot{V}O_2$ values increased with a rise in τ_{off} (0.5 min (—), 1.0 min (×), 2.0 min (▲) and 3.0 min (□)). The lower panel shows a comparison of the difference ($\Delta\dot{V}O_2$) between oxygen uptake estimated while changing the τ_{off} and that estimated from the relationship of $\dot{V}O_2$ -WR obtained below 50 W in DLE starting from 240 W.

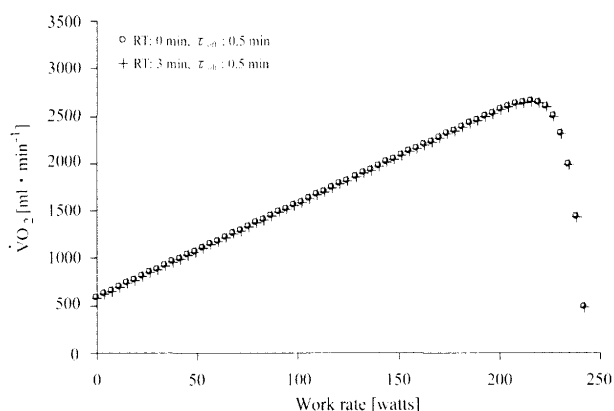


Fig. 6 Kinetics of oxygen uptake ($\dot{V}O_2$) estimated by the numerical computation model in which the interval of subdivision (RT) is set to 0 min (○) and 3 min (+) and both time constants (τ_{on} and τ_{off}) are fixed at 0.5 min.

220 W was the same in all RT conditions. However, estimated $\dot{V}O_2$ showed a higher value from 220 to 130 W in the high-power output phase accompanied by a fall in RT. The peak value of $\dot{V}O_2$ was about 3000 ml·min⁻¹. $\dot{V}O_2$ progressively decreased after reaching a peak. In the period below about 100 W, $\dot{V}O_2$ were similar in all RT conditions. In all RT conditions, $\Delta\dot{V}O_2$ in DLE₂₄₀ showed a negative value at the

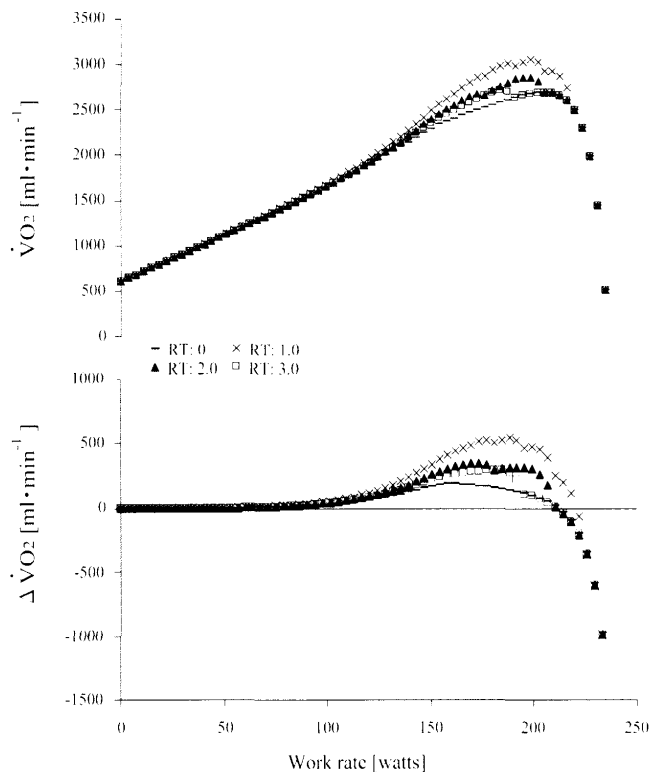


Fig. 7 Kinetics of oxygen uptake ($\dot{V}O_2$) estimated by the numerical computation model in which time constant during recovery (τ_{off}) is fixed at 2.0 min and the interval of subdivision (RT) is set to 0 (—), 1.0 (×), 2.0 (▲) and 3.0 min (□) (upper panel). The lower panel shows a comparison of the difference ($\Delta\dot{V}O_2$) between oxygen uptake estimated while changing the interval of subdivision (RT) and that estimated from the relationship of $\dot{V}O_2$ -WR obtained below 50 W in decremental load exercise starting from 240 W.

onset of exercise and shifted to a positive value in response to a decrease in WR. The peak value of $\Delta\dot{V}O_2$ was about 520 ml·min⁻¹. $\Delta\dot{V}O_2$ progressively decreased toward the zero ml·min⁻¹ after showing a peak. Similarly, $\Delta\dot{V}O_2$ in DLE₁₂₀ showed a negative value at the onset of exercise. However there was no positive value in DLE₁₂₀.

In measured $\dot{V}O_2$, the slope of the $\dot{V}O_2$ -WR relationship in DLE₂₄₀ was 14.77 ml·min⁻¹·W⁻¹ at the high-power output phase and decreased to 10.17 ml·min⁻¹·W⁻¹ at the low-power output phase. Similarly, in estimated $\dot{V}O_2$, the slope of the $\dot{V}O_2$ -WR relationship in DLE₂₄₀ was 14.60 ml·min⁻¹·W⁻¹ at the high-power output phase and decreased to 10.17 ml·min⁻¹·W⁻¹ at the low-power output phase. These slopes approximated to the measured one.

The optimal values of τ_{off} and RT for the numerical computation model were 2.8 min and 3.0 min, respectively. The upper panel in Fig. 8 shows $\dot{V}O_2$ kinetics estimated by the numerical computation model in which τ_{off} is set to 2.8 min and RT is set to 3.0 min. $\dot{V}O_2$ kinetics was the same quantitatively. The peak value of $\dot{V}O_2$ was about 2800 ml·min⁻¹. $\dot{V}O_2$ progressively decreased after achieving peak value. Both $\Delta\dot{V}O_2$ showed a negative value at the onset of exercise and shifted to a positive value in response to a decrease in WR. The peak value of $\Delta\dot{V}O_2$ was about

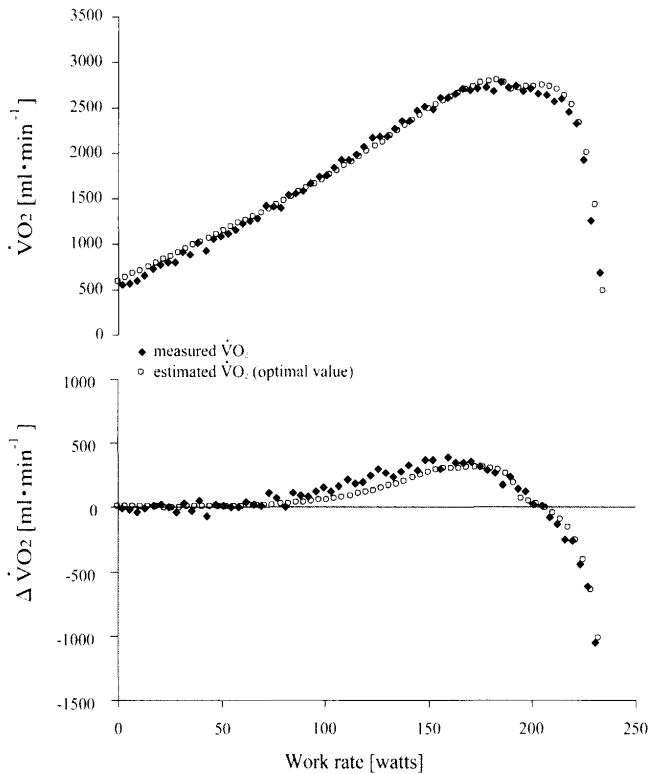


Fig. 8 Comparison of the oxygen uptake ($\dot{V}O_2$) simulated by the numerical computation model using the optimal value (○) with measured $\dot{V}O_2$ (◆) is shown in the upper panel. The lower panel shows a comparison of the difference between oxygen uptake simulated and that measured from the power output below $\dot{V}O_2$ -WR relationship obtained below 50 W in decremental load exercise starting from 240 W.

$350 \text{ ml} \cdot \text{min}^{-1}$. $\Delta\dot{V}O_2$ progressively decreased toward the zero $\text{ml} \cdot \text{min}^{-1}$ after showing a peak.

Discussion

The slope of the $\dot{V}O_2$ -WR relationship obtained within the low-power output phase (0–50 W) was $10.57 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$ in DLE_{120} (below the VT). This slope value is close to that reported in CLE and ILE (Hansen et al., 1987; Barstow and Mole, 1991). This slope was used to estimate $\dot{V}O_2$ at a given high power output. The difference ($\Delta\dot{V}O_2$) between estimated $\dot{V}O_2$ and measured $\dot{V}O_2$ was negative at the onset of exercise and was $0 \text{ ml} \cdot \text{min}^{-1}$ after 90 W. This result indicates that $\dot{V}O_2$ in DLE starting from below the VT did not include the excess $\dot{V}O_2$. In contrast, the slopes were $14.77 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$ in the high-power output phase and $10.61 \text{ ml} \cdot \text{min}^{-1} \cdot \text{W}^{-1}$ in the low-power output phase. The slope in the low-power output phase in DLE_{240} was equal to the slope in DLE_{120} . In addition, $\Delta\dot{V}O_2$ in DLE_{240} was positive in a period from 200 to 100 W. This result indicates that $\dot{V}O_2$ in DLE starting from above the VT includes excess $\dot{V}O_2$.

To determine whether excess $\dot{V}O_2$ is explained by O_2 debt, $\dot{V}O_2$ in DLE_{240} was simulated. As shown in Fig. 4, simulated $\dot{V}O_2$ and measured $\dot{V}O_2$ were plotted against WR. In this simulation model, τ_{off} value was same as τ_{on} (0.5 min,

symmetrical model). It was shown that the estimated $\dot{V}O_2$ and measured $\dot{V}O_2$ were the same at the onset of exercise. Measured $\dot{V}O_2$ values were higher than estimated $\dot{V}O_2$ values in a period from 200 to 100 W. However, the values were the same below 100 W. This result indicated that $\dot{V}O_2$ simulated by the numerical computation model using the same time constant could not express excess $\dot{V}O_2$ in the high-power output phase. Therefore, as shown in Fig. 4, we tried to express excess $\dot{V}O_2$ by changing τ_{off} in all steps (asymmetrical model). The newly simulated $\dot{V}O_2$ kinetics was similar to measured $\dot{V}O_2$ kinetics only at the onset of exercise. But $\dot{V}O_2$ simulated by the asymmetrical model was greater than $\dot{V}O_2$ simulated by the symmetrical model.

Then, we employed the mixed model of asymmetry and symmetry. Exercise intensity in DLE starting from a high WR gradually decreases with time and finally comes below the VT. When exercise intensity rises rapidly at the onset of exercise, recruitment of anaerobic energy and fast-twitch muscle fibers is required. However, it is thought that the muscle fiber recruitment pattern in DLE changes from fast-twitch fibers to slow-twitch fibers with decrement in exercise intensity. It has also been reported that the time constant of fast-twitch fibers shows a high value compared with that of slow-twitch fibers (Barstow et al., 1996). Moreover, it has been reported that $\dot{V}O_2$ kinetics during the recovery phase in CLE shows different responses depending on exercise intensity (Rossiter et al., 2002). Therefore, we assumed that $\dot{V}O_2$ kinetics in DLE is symmetry below the VT and asymmetry above the VT. It has been reported that the time constant of onset of exercise (τ_{on}) below the VT differs among subjects and that the relationship between τ_{on} and exercise intensity shows nonlinearity (Brittain et al., 2001). However, Yano et al. (2003) confirmed that a simulation model in which τ_{on} is set symmetrically in a step below the VT was valid for approximating $\dot{V}O_2$ in DLE starting from low-intensity exercise. Therefore, it seems that a symmetrical model below the VT is useful for approximating $\dot{V}O_2$. Although the mixed model based on this assumption made it possible to express an excess $\dot{V}O_2$, the excess $\dot{V}O_2$ was lower than measured excess $\dot{V}O_2$. And so, we attempted to express the excess $\dot{V}O_2$ by adding a subdivision model.

The physiological basis of the subdivision model is as follows. Motor unit substitution during prolonged isometric contraction is reported (Westgarrd et al., 1999). Moreover, Kouzaki et al. (2002) quantified the frequency of alternate muscle activity and the influence of different exercise intensities between the knee extensor synergists during low-level prolonged contraction. According to their results, during low-level prolonged contraction, alternate muscle activity in quadriceps muscle appeared only between the rectus femoris (RF) and vastus lateralis (VL) or vastus medialis (VM), and it has been reported that alternate muscle activity emerges under the condition of sustained contraction with force production levels $<5.0\%$ of MVC.

As shown in Figs. 6 and 7, however, $\dot{V}O_2$ simulated by the numerical computation model in which the interval of

subdivision (RT) is set to 0–3 min did not vary unless using an asymmetrical model. Therefore, it was indicated that excess $\dot{V}O_2$ was related to O_2 debt and subdivision of a step. In addition, although $\dot{V}O_2$ simulated by the subdivision model were the same as measured $\dot{V}O_2$ at both onset of exercise and low-power output phase, simulated $\dot{V}O_2$ showed a higher value from 220 to 130 W in the high-power output phase with decreased RT. This result suggests that accumulation of O_2 debt influences excess $\dot{V}O_2$.

The optimal values of τ_{off} and RT for the numerical computation model were 2.8 min and 3.0 min, respectively. However, $\dot{V}O_2$ simulated by these optimal values did not completely coincide with measured $\dot{V}O_2$ in DLE starting from above the VT.

There are two possible reasons for this discrepancy. One is related to a parameter of the model. Although it was possible to consider the slow component of $\dot{V}O_2$ (phase III) reported in recent studies, $\dot{V}O_2$ exponential function of the model may be complicated. Another reason is that the optimal value of τ_{off} exceeded the value (0.5–1.0 min) reported in previous works which examined recovery kinetics of the creatine phosphate response (Rossiter et al., 2002) and $\dot{V}O_2$ (Özyener, 2000). If $\dot{V}O_2$ kinetics after the end of a heavy exercise is approximated by a single exponential function consisting of a fast phase and a slow phase, the composition ratio of each phase will be expressed as x and y in the equation 9. Here, the fast decrease phase is $x\%$ and the slow decrease phase is $y\%$.

$$0.5 \times x + 2.8 \times y = 0.75 \quad (9)$$

$$(\because x + y = 1)$$

The values of 0.5 and 0.75 min are τ_{off} of moderate and heavy intensity, respectively. If this equation is solved, x will be about 0.11 and y will be about 0.89. According to this result, it is thought that 10% of the kinetics of $\dot{V}O_2$ after heavy exercise is fast phase and 90% is slow phase. Therefore, the time constant calculated by the present study may be higher than the value of τ_{off} reported by previous works.

In summary, to examine the relationship between excess $\dot{V}O_2$ in DLE₂₄₀ and O_2 debt, we examined $\dot{V}O_2$ in DLE starting from a WR above the VT using a numerical computation model. The primary results of this study demonstrate that $\dot{V}O_2$ simulated by our numerical computation model is qualitatively approximated to measured $\dot{V}O_2$, although simulated $\dot{V}O_2$ was quantitatively insufficient for approximating measured $\dot{V}O_2$. This quantitative difference may be derived from the slow component of $\dot{V}O_2$ (phase III) reported by CLE and/or the subdivision interval in a step.

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