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A Mathematical Analysis of the Oxygen Uptake after Strenuous Exercise

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Oxygen uptake before and after strenuous exercise for about one minute was determined in 5 healthy male subjects at comfortable (18°C db) and hot (35°C db) room temprature. It was assumed that the oxygen uptake during recovery could be fitted best by an equation of the form, $Y = c + a_1 \exp(-k_1 t) + a_2 \exp(-k_2 t)$, where Y is the oxygen uptake during recovery at any time (t). The term $a_1 \exp(-k_1 t)$ and $a_2 \exp(-k_2 t)$ presumably represent the alactic and lactic components, the amount of alactic and lactic oxygen debt is equal to a_1/K_1 and a_2/k_2. In this study the each constant in above equation was determined by the least squares method. It was found that there are no statistical difference between 18°C and 35°C in not only exponential curve parameters, but also alactic, lactic and total oxygen debts, while total oxygen debt at 35°C was higher in 3 out of 5 subjects.

Since oxygen debt was defined by Hill et al. (8), the kinetics of oxygen uptake during excercise and recovery have been investigated frequently. However, one of the major problem at present is the reliability in the measurement of the maximum oxygen debt which indicates anaerobic work capacity in man; values raging from 10 to 20 liters have been reported for human subjects (18), but Margaria et al. (15) in a detailed analysis, have suggested that the maximum value for the oxygen debt should only be about 4 liters. Furthermore, Kuroda et al. (13) determined the daily variation of the maximum oxygen debt in sprinter and long distance runners. They found that the average of the difference between the maximum and minimum values and coefficient variations were 28.0% and 10.8%, respectively. From these results, they also pointed out that one of the reason of daily variation is the size of what we call base line. It seems to be reasonable to assume that the cause of intraindividual variation of the oxygen debt may be related to variation of the base line by the difference of experimental room temperature (2, 9).

On the other hand, Hill et al. (8) have suggested that the oxygen debt was due to the elimination of lactic acid produced during exercise. After that it has been reported by Margaria et al. (14) that the payment of the oxygen debt from muscular exercise can not be explained solely by lactate; they have distinguished the two mechanisms of the oxygen bebt, the one due to the lactic acid, and an alactic one where there is no apparent lactic acid formation. Although oxygen debt have been estimated using a few mathematical equations by the several authors (4, 6, 7, 10, 11, 12, 17, 21), these investigators determined the alactic and/or lactic oxygen debt by way of keep the size of the some constant in equation or eye measurement, but not the so-called the method of least squares; it will be impossible

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to compare the effect of environmental temperature on the oxygen debt which was obtained by means of previous authors.

The present study was made to estimate the alactic and lactic oxygen debt by adequate mathematical model, and to obtain further information about the effect of environmental temperature on the oxygen debt.

Methods

The subjects were 5 healthy males (laboratory staffs) aged 25 to 33 years. They have experience in maximal exercise. Physical data of the subjects and their maximal oxygen uptake are shown in Table 1. All experiments were performed on the motor driven treadmill in climatic chamber under controlled temperature (18 ± 1.0°C db and 35 ± 1.0°C db) and humidity (60 ± 3% R. H.) conditions. The subjects came to the laboratory at least three times on the separate days, and only one maximal exercise test was conducted using treadmill with constant grade of 8.6%. On the first day, maximum oxygen uptake of each subject was determined by the incremental loading technique at constant temperature and humidity (18°C db and 60% R. H.). Details of the technique have been published elsewhere (16). On the other hand, measurement of oxygen debt was done on the second and third days; oxygen uptake during rest, exercise and recovery were determined by the Douglas bag method at comfortable room temperature (18 ± 1.0°C db) on the second day, and at hot room temperature (35 ± 1.0°C db) on the third day, respectively. Expired gas was collected by the Douglas bag for 5 min after the subject rested for 30 minutes at supine position. Maximal exercise was conducted using the treadmill with constant grade of 8.6%. The speed of the treadmill was chosen so that the subject could run for about 60 seconds before exhaustion. Expired gas was collected with 20 second intervals during exercise up to exhaustion. In recovery, it was collected at 30 second intervals during the 2nd min, one minute intervals to 4th min, and two minute intervals to 10th min, 5 minute intervals to 30 min, and 10 minute intervals until 60 min, respectively. The volume of collected air was measured by wet-gasometer, and gas analysis was performed using an infrared CO_2 analyzer (Godart, Capnograph) and oxygen analyzer (Morgan, Model 262 D). These apparatus were calibrated frequently with two calibration gases that had been checked by the Scholander micro-gas analyzer.

Table 1. Physical characteristics of subjects.

Subjects	Age (yr)	Height (cm)	Weight (kg)	$\dot{V}o_{2\,max}/W$ (ml/kg·min)
M. S.	33	168	59	55.9
C. Y.	25	156	53	64.1
F. N.	29	170	71	45.6
Y. N.	33	166	62	60.0
N. S.	28	165	62	49.8

$\dot{V}o_{2\,max}/W$; maximum oxygen uptake per kilogram of body weight.

We assumed that oxygen uptake during recovery could be fitted best by an equation of the form $Y = c + a_1 \exp(-k_1 t) + a_2 \exp(-k_2 t)$, where Y is the oxygen uptake during recovery at any time (t). The term $a_1 \exp(-k_1 t)$ and $a_2 \exp(-k_2 t)$ presumably represent the alactic and lactic components, the amount of alactic and lactic oxygen debt is equal to a_1/k_1 and a_2/k_2 (10). The parameters in above formula were estimated by the least squares method using NOVA 1200 computer.

Adaptation procedure for

$$Y = a_0 + a_1 \exp(-a_2 x) + a_3 \exp(-a_4 x) \qquad (a_2 > a_4)$$

$a_0 = c$
$a_1 = a_1$
$a_2 = k_1$
$a_3 = a_2$
$a_4 = k_2$

Suppose we have a set of n measured pairs x_i, y_i, $i = 1$, ———, n we try to adapt to above function.
Define:

$$y(x_i) = a_0 + a_1 \exp(-a_2 x_i) + a_3 \exp(-a_4 x_i) \tag{1}$$

for a given set of parameters a_0, ———, a_4. Adaptation in terms of a least-squares fit is reached by searching the point at which the sum of square difference is minimum in the parameter space.

$$S^2 (a_0, \text{———}, a_4) = \sum_{i=1}^{n} (y_i - y(x_i))^2 \tag{2}$$

The minimum value of S^2 can be determined by setting the derviatives of S^2 with respect to the parameters equal to 0;

$$\frac{\partial S^2}{\partial a_k} = 0 \quad k = 0, \text{———}, 4 \tag{3}$$

(This is a set of 4 non-linear equations).
However, it is difficult to solve these equations directly because of non-linearlity of the function S^2 with parameter a_k. Then we expand the function S^2 to first order in a Taylor's series expansion as a function of the parameter a_j

$$S^2 = S_0^2 + \sum_{i=0}^{4} \left(\frac{\partial S_0^2}{\partial a_j} \delta a_j\right) \tag{4}$$

where S_0^2 is the value of S^2 at some starting point and in where the values of the parameters are a'_j

$$S_0^2 = \sum_{i=1}^{n} (y_i - y'(x_i)) \tag{5}$$

where $y'(x_i)$ is

$$y'(x_i) = a'_0 + a'_1 \exp(-a'_2 x_i) + a'_3 \exp(-a'_4 x_i) \tag{6}$$

and the δa_j are increments in the parameter a_j to reach the point at which y(x) and S^2 are to be evaluated.
To substitute (4) into (3) lead to:

$$\frac{\partial S^2}{\partial a_k} = \frac{\partial S_0^2}{\partial a_k} + \sum_{j=0}^{4} \left(\frac{\partial^2 S_0^2}{\partial a_j \partial a_k} \delta a_j\right) = 0$$

$$k = 0, \text{———}, 4 \tag{7}$$

The result is a set of 4 simultaneous linear equations in δa_j.
Defining the matrix α and β as

$$\beta_k = -\frac{1}{2} \frac{\partial S_0^2}{\partial a_k} \qquad j, k = 0, \text{———}, 4$$

$$\alpha_{jk} = \frac{1}{2} \frac{\partial^2 S_0^2}{\partial a_j \partial a_k}$$

(7) can be written as a matrix equation,

$$\beta_k = \sum_{j=0}^{4} (\delta a_j \alpha_{jk}) \qquad k = 0, \text{———}, 4$$

(or)

$$\beta = \delta a \alpha$$

with the inverted matrix ϵ of α we can solve the equation

$$\delta a = \beta \epsilon \qquad (8)$$

$$\epsilon = \alpha^{-1} \qquad (9)$$

and the approximate solutions of (3) are

$$a_k = a'_k + \delta a_k \qquad k = 0, ---, 4 \qquad (10)$$

It can be shown that iterative recalculation of a_k by (8) and (10) always lead to the solution of (3) if the starting point is close enough to the (minimum) point where S^2 is minimum. Furthermore, the "standard errors" in a_k (σa_k) can be calculated from

$$\sigma^2_{a\,k} = \epsilon_{kk} \frac{S^2}{n-5} \qquad k = 0, ---, 4 \qquad (11)$$

Results

The mean value and standard deviations of exhaustion time at comfortable and hot room temperatures were 67.8 ± 12.8 and 69.2 ± 11.0 seconds, respectively. The difference between these two values was statistically not significant.

Fig. 1 shows the measured values of the oxygen uptake during recovery period in the case of subject M. S. together with fitted curve ($Y = c + a_1 \exp(-k_1\ t) + a_2 \exp(-k_2\ t)$). The left pannel represents the results of the comfortable room temperature, the right ones these of the hot temperature. Despite slightly scatter of the fitted curve, it agreed very closely with experimental values. The same result was observed by testing another 4 persons.

Table 2 demonstrates the individual's constants at comfortable and hot room temperature estimated by the least-squares method. As shown in Table 2, the standard errors of a_2 and k_2 (Sa_2 and Sk_2) were a little higher than that of a_1, k_1 and c (Sa_1, Sk_1 and Sc). The mean and standard deviations of the each constant in equation, and of alactic, lactic and total oxygen debt are given in Table 3. Student's t-test was applied between the mean value of each variable, and its results are also shown in Table 3. It was found that the average values of alactic oxygen debt at the comfortable and hot room temperature were 1.71 and 1.42 liters. The difference between the two values was small and statistically not

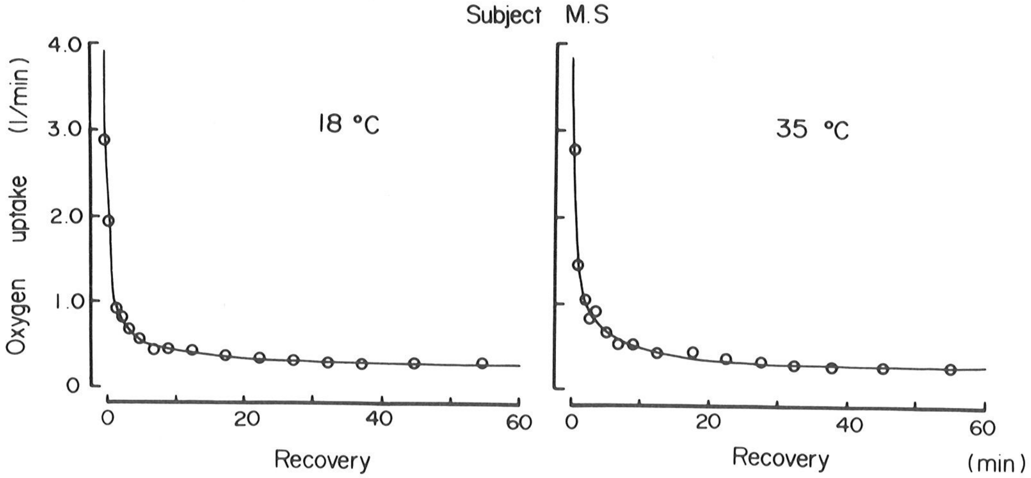

Figure 1. Oxygen uptake during recovery after strenuous exercise at comfortable (left) and hot (right) room temperatures. Open circles and solid lines were measured values and fitted curves obtained from the each constant in equation ($Y = c + a_1 \exp(-k_1\ t) + a_2 \exp(-k_2\ t)$), respectively.

Table 2. The results of exponential curve parameters for calculation of equation $Y = c + a_1 \exp(-k_1 t) + a_2 \exp(-k_2 t)$.

Subjects	Room temperature (°C)	a_1 ($L \cdot min^{-1}$)	Sa_1	k_1 (min^{-1})	Sk_1	a_2 ($L \cdot min^{-1}$)	Sa_2	k_2 (min^{-1})	Sk_2	c ($L \cdot min^{-1}$)	Sc
M. S.	18	3.351	0.307	1.663	0.173	0.487	0.309	0.098	0.077	0.275	0.063
	35	2.679	0.234	1.733	0.134	0.737	0.316	0.116	0.041	0.289	0.039
C. Y.	18	2.029	0.088	1.532	0.064	0.522	0.154	0.110	0.026	0.254	0.017
	35	2.371	0.068	1.317	0.051	0.349	0.083	0.099	0.027	0.263	0.015
F. N.	18	1.894	0.098	0.833	0.101	0.528	0.091	0.086	0.031	0.311	0.024
	35	1.472	0.155	1.383	0.167	1.009	0.312	0.176	0.036	0.350	0.020
Y. N.	18	2.425	0.092	1.257	0.088	0.436	0.134	0.093	0.041	0.296	0.029
	35	2.234	0.122	1.732	0.051	0.552	0.163	0.079	0.018	0.283	0.027
N. S.	18	1.747	0.289	1.733	0.459	0.930	0.860	0.270	0.135	0.294	0.027
	35	2.350	0.095	1.729	0.065	0.533	0.149	0.135	0.027	0.291	0.014

Table 3. Statistical difference of the mean values of 18°C and 35°C and the corresponding probability.

Room Temp. (°C)		a_1 ($L \cdot min^{-1}$)	k_1 (min^{-1})	a_2 ($L \cdot min^{-1}$)	k_2 (min^{-1})	c ($L \cdot min^{-1}$)	Alactic 0_2 debt (L)	Lactic 0_2 debt (L)	Total 0_2 debt (L)
18	mean	2.289	1.403	0.580	0.131	0.286	1.709	4.797	6.506
	± SD	.576	.328	.017	.070	.020	.468	.857	1.287
35	mean	2.241	1.578	0.636	0.121	0.295	1.423	5.309	6.732
	± SD	.405	.187	.223	.033	.030	.243	1.350	1.260
	$p <$	0.90	0.30	0.80	0.80	0.40	0.50	0.50	0.80

significant. Also the average values of lactic oxygen debt at 18°C and 35°C were 4.80 and 5.31 liters, with difference being statistically not significant. The ranges of calculated total oxygen bedt at comfortable and hot room temperature were from 4.45 to 8.41 and from 5.23 to 7.90 liters, respectively. It was observed that the total oxygen debt at 35°C was higher in 3 out of 5 subjects, and that average total oxygen debt at 18°C and 35°C were 6.51 and 6.73 liters. The difference in total oxygen debt observed at 18°C and 35°C was again statistically not significant.

Discussion

Since Margaria et al. (14) first suggested that the oxygen debt can be devided into two components that were described as the sum of the exponential term, the alactic and lactic oxygen debt has hitherto been mathematically evaluated by the several authors (4, 6, 7, 10, 12, 17, 21). As described previously, however, these authors did not determined the alactic and/or lactic oxygen debt by the adequate mathematical procedure; Sidney and Shephard (21) arbitrarily devided the overall curve into two components, basing the lactate slope on measurement made between the second and 15th min of recovery periods. Henry and Demoor (6) have reported that recovery data from 690 and 920 kg·min (115 and 153 watt) exercise show satisfactory fit with a two cmoponents system of the formula ($Y = c + a_1 \exp(-k_1 t) + a_2 \exp(-k_2 t)$) using same velocity constants for both sets of data. Katch et al. (10) and Katch (11) obtained the each constants in above equation as constant c is equal to resting oxygen uptake which was measured before exercise. In addition, Knuttgen (12) have analyzed for two components from recovery data using Prony's method for approximation in the equation; $P_x = c_1 + c_2 (r_1)^x + c_3 (r_2)^x$, where $r_1 = e^{b}_{1}$ and $r_2 = e^{b}_{2}$, the exponents were solved first and then the coefficients were obtained, both by the least squares process. However, according to Knuttgen, to determine the exponents, a single nonlinear equation was solved which, for approximations of the type considered, turned out to be quardratic; as the method for approximations requires equally spaced abscissa values, it is necessary to incorporate an interpolation routine in order to obtain such spacing.

It is of course impossible to compare the oxygen debt at comfortable and hot environmental temperatures using method of previous authors. To compare the oxygen debt determined in various conditions, it will be necessary to establish the method determining alactic, lactic and total oxygen debt by the adequate mathematical model. As described above, we assumed in this study that oxygen uptake during recovery could be fitted best by one formula, $Y = c + a_1 \exp(-k_1 t) + a_2 \exp(-k_2 t)$. Moreover we determined each constants in above equation using complete least squares method. It was found that the standard errors of a_2 and k_2 was a littel higher than that of a_1, k_1 and c as shown in Table 2. This seems mainly to be due to the numbers of measured oxygen uptake; it may be more small if oxygen uptake during recovery period was measured more details.

In this study the average value and standard deviations of the fast component velocity constant, k_1, at 18°C and 35°C were 1.403 ± 0.328 and 1.578 ± 0.187. This values appeared to be agree with range reported for human subjects during heavy exercise (21), but it is about the 1/2 of the evaluated by Royce (20) who measured k_1 in 2/3 max work load. These results suggested that k_1 value may be change more or less with work load, though Berg (1) have reported that k_1 is independent of work load.

On the other hand, Brooks et al. (2) observed that in the rats increasing temperature had a striking effect on mitochondrial function of skeletal muscle. Consolazio et al. (3) measured the oxygen uptake of healthy young men at three different levels of room temperature, 21.2, 29.4 and 37.7°C. They found that the oxygen uptake 37.7°C was higher than at 21.2 and 29.4°C, while there are no significant difference between 21.2 and 29.4°C. Hori et al. (9) reported the sum of oxygen uptake for 20 minutes after submaximal bicycle work of 600 kg·min was significantly larger in 30°C than in 23°C. Contrary, Dill et al. (5) and Rowell et al. (19) observed no significant difference in oxygen uptake during submaximal exercise at hot (34 and 43.3°C) and cold (12 and 25.6°C) room temperature. It was found in this study that there are no statistical difference between 18 and 35°C in not only exponential curve parameters, but also alactic and lactic and total oxygen debt, while total oxygen debt at 35°C was higher in 3 out of 5 subjects. From these results, it was suggested that the oxygen debt after strenous exercise for short time does not effect by the acute change of room temperature at least under conditions as applied here. However, it is uncertain whether there are difference in the oxygen debt between 18 and 35°C if the subject was stayed in climatic chamber for more long time than that of this experiment. The question also arises as to whether c value, which is one the determinant of oxygen debt, is really a constant over the recovery periods. Since variation of c value may be related to the threshold for change of environmental temperature (3), the relationship between oxygen debt and environmental temperature will be need further investigation.

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References

1) Berg, W. E. Individual differences in respiratory gas exchange during recovery from moderate exercise. *Amer. J. Physiol.* **149**: 597 – 610, 1947.
2) Brooks, G. A., K. J. Hittelman, J. A. Faulkner, and R. E. Beyer. Temperature, skeletal muscle mitochondrial functions, and oxygen debt. *Amer. J. Physiol.* **220**: 1053 – 1059, 1971.
3) Consolazio, C. F., L. R. O. Matoush, R. A. Nelson, J. B. Torres, and G. J. Isaac. Environmental temperature and energy expenditures. *J. Appl. Physiol.* **18**: 65 – 68, 1963.
4) Demoor, J. C. Individual differences in oxygen debt curves related to mechanical efficiency and sex. *J. Appl. Physiol.* **6**: 460 – 466, 1954.
5) Dill, D. B., H. T. Edwards, P. S. Bauer, and E. J. Levenson. Physical performance in relation to external temperature. *Arbeitsphysiol.* **4**: 508 – 518, 1931.
6) Henry, F. M. and J. Demoor. Metabolic efficiency of exercise in relation to work load at constant speed. *J. Appl. Physiol.* **2**: 481 – 487, 1950.
7) Henry, F. M. Aerobic oxygen consumption and alactic debt in muscular work. *J. Appl. Physiol.* **3**: 427 – 438, 1951.
8) Hill, A. V., C. N. H. Lond, and H. Lupton. Muscular exercise, lactic acid and supply and utilization of oxygen. Proc. Roy. Soc. London B. **97**: 84 – 138, 1924.
9) Hori, S., J. Tsujita, and H. Yoshimura. Energy requirements of men during exercise in a hot environment and a comfortable environment. *J. Physiol. Soc. Jap.* **38**: 507 – 509, 1976.
10) Katch, F. I., R. N. Girandola, and F. M. Henry. The influence of the estimated oxygen cost of ventilation on oxygen deficit and recovery oxygen intake for moderately heavy bicycle ergometer exercise. *Med. Sci. Sports,* **4**: 71 – 76, 1972.
11) Katch, V. L. Kinetics of oxygen uptake and recovery for supramaximal work of short duration. *Inter. z. angew. Physiol.* **31**: 197 – 207, 1973.
12) Knuttgen, H. G. Oxygen debt after submaximal physical exercise. *J. Appl. Physiol.* **29**: 651 – 657, 1970.
13) Kuroda, Y., K. Tsukagoshi, T. Amamiya, Y. Suzuki, and S. Itoh. A study of the measurement of maximum oxygen debt (In Japanese). Scientific Report of Japan Amature Sports Association. **10**: 1 – 19, 1974.
14) Margaria, R., H. T. Edwards, and D. B. Dill. The possible mechanism of contracting and paying the oxygen debt and role of lactic acid in muscular contraction. *Amer. J. Physiol.* **106**: 689 – 715, 1933.

15) Margaria, R., P. Cerretelli, P. E. Di Prampero, C. Massari, and G. Torelli. Kinetics and mechanism of oxygen debt contraction in man. *J. Appl. Physiol.* **18**: 371 –377, 1963.

16) Miyamura, M. and Y. Honda. Oxygen intake and cardiac output during maximal treadmill and bicycle exercise. *J. Appl. Physiol.* **32**: 185 – 188, 1972.

17) Roberts, A. D. and A. R. Morton. Total and alactic oxygen debts after supramaximal work. Eurp. *J. Appl. Physiol.* **38**: 281 – 289, 1978.

18) Robinson, S., D. L. Robinson, R. J. Mountjoy, and R. W. Bullard. Influence of fatigue on the efficiency of men during exhausting runs. *J. Appl. Physiol.* **12**: 197 – 201, 1958.

19) Rowell, L. B., H. J. Marx, R. A. Bruce, R. D. Conn, and F. Kusumi. Reductions in cardiac output, central blood volume, and stroke volume with thermal stress in normal men during exercise. *J. Clin. Invest.* **45**: 1801 – 1816, 1966.

20) Royce, J. Active and passive recovery from maximal exercise capacity work. *Inter. z. angew. Physiol.* **28**: 1 – 8, 1969.

21) Sideny, K. and R. J. Shephard. Physiological characteristics and performance of the whitewater paddler. Europ. *J. Appl. Physiol.* **32**: 55 – 70, 1973.

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