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Kinetics of Oxygen Uptake and Recovery for Supramaximal Work of Short Duration

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Abstract. In order to follow the time pattern of oxygen uptake and recovery for supramaximal work of short duration, 35 male subjects (mean age 21.4 years, mean body weight 71.9 kg) pedalled a bicycle ergometer at maximal speed for 1 min. A constant frictional resistance of 5.5 kg was used, resulting in a total work output of 2890 kpm (85 revolutions, SD = 7.5). The total percent decrement in work output from the initial rate on this test was 59.7 %. The total oxygen uptake during the work averaged 2.35 l, the net oxygen recovery was 4.89 l, while the net work efficiency was 19.3 %. One and two component exponential curves fit the observed oxygen uptake and recovery measures with a high degree of accuracy. Comparison of the curve parameters with published data showed large differences for the post exercise oxygen recovery and the slow component of the recovery curve. The magnitude of the fast component of recovery was similar to other data. The total oxygen uptake during the test was found to be 10% lower than the maximal oxygen uptake determined on a seperate progressive step-increment test. It was shown, by curve analysis, that the maximal oxygen uptake would have been reached in approximately 2 min.

Key words: O_2 Uptake — O_2 Debt — Supramaximal Work.

The kinetics of oxygen uptake during exercise and recovery have been studied for light [2, 9, 13, 15, 28, 34], moderate [7, 8, 14, 16, 21, 24, 26], and moderately heavy work [16, 19, 23, 25] of various durations. Depending on the intensity of the exercise, either a single or double component exponential equation has been found to describe the time pattern of oxygen uptake during the exercise and subsequent recovery. The derivation and explanation of the exponential formula can be found in several reports [9, 15, 16, 20, 26, 34]. Briefly, the equation states that the rate of oxygen uptake (Y) at any time t of exercise is given by the equation:

$$Y = C - a_1 e^{-k_1 t} + a_2 e^{-k_2 t}, \qquad (1)$$

where, C is the resting oxygen uptake $+ (a_1 + a_2)$, $a_1 + a_2$ represent the steady-level oxygen uptake above rest, and the exponentials equal the amount of oxygen uptake. During recovery, the negative term changes to positive, C equals resting oxygen uptake, $a_1 + a_2$ represents the amount of oxygen uptake at $t = 0$ (end of exercise and beginning of recovery), and the exponentials represent the fast and slow pay-off components first described by Hill *et al.* [16] and Margaria *et al.* [26].

In the 1920's interpretation of the exponential uptake and recovery curves were based on the assumed time course of lactate accumulation and disappearance [16]. In 1933, Margaria [26] *et al.* demonstrated that the fast component of the recovery curve was not responsible for this lactate disappearance but was related to the oxidation of substances furnishing the energy for the resynthesis of phosphagens split during muscular contraction.

The fast component ($a_1 e^{-k_1 t}$), which has been shown to be approximately a linear function of the oxygen uptake in exercise [14, 26], as well as the slower 'lactacid' component ($a_2 e^{-k_2 t}$) have been studied by numerous investigators for light to moderate work [1, 3, 8, 20, 21, 24, 27, 29, 33]. There are, however, very little data on the magnitude of these two exponential components, as well as the time pattern of oxygen uptake during exercise and recovery for extremely heavy work (supra maximal work) of short duration where only a very small portion of the energy requirement is met by aerobic metabolism. It has been pointed out by Margaria [24] that during such work (as for example cycling against a very heavy resistance at maximal speed for 40 to 60 sec) an individual will reach his anaerobic capacity. Thus, it is possible that the kinetics of oxygen uptake for this exercise and recovery will be quite different than it is for light or moderately heavy exercise conditions, possibly due to such factors as increased lactate production [23], extra oxygen cost of ventilation [32], or increased temperature during recovery [3].

Therefore, the aim of the present study is to examine the kinetics (time pattern) of oxygen uptake during exercise and recovery for supramaximal work of short duration.

Methods

Subjects. Thirty-five male college students served as subjects. The mean age was 21.4 years (SD = 2.4) and mean weight 71.9 kg (SD = 7.5). These were all volunteer subjects from the general physical activities program of the University. Students involved in intercollegiate athletics, or who were participating in a conditioning program were omitted from the sample.

Supramaximal Work of Short Duration. Each subject rode a Monarch bicycle ergometer (Sweden) for 1 min as fast as possible with a constant frictional resistance of 5.5 kg/revolution. The choice of this workload was based on the observation that subjects are able to accomplish more work perunit time with this particular rate-profile (resistance × pedal frequency) than one involving a greater or lesser frictional resistance, and hence, a different number of pedal revolutions (B. Edwards, unpublished data). Also, the data of Margaria *et al.* [23, 24] suggests that if individuals work as rapidly as possible for 40 to 60 sec at a comparable work-rate, the anaerobic capacity will be attained.

Prior to the beginning, and during the test, the subjects were not told the exact duration of the test, only that it was very short and they were to attempt to turn as many revolutions as possible. This is important since preliminary data indicated that when subjects know the duration of the work, they tend to pace themselves and don't produce an initial all-out effort.

Starting with the pedals in a horizontal position with minimal friction, on the command *Ready-Go*, the subjects began pedalling as fast as possible. The frictional resistance was immediately increased to the desired setting and remained through out the test. It was necessary to start at zero friction because of the difficulty in overcoming the inertial factors with such a high frictional resistance. The time delay from the command *Go* to the setting of the proper friction load was 1 to 2 sec. An electrical counter activated by each pedal revolution made it possible to monitor the exact work-rate profile of each subject.

Expired air samples were continuously collected by the open circuit method described elsewhere [18], during 2 min of rest, during exercise, and for 15 min of recovery. The number of aliquot samples of expired air and time of collection were:

2—1 min resting samples;
3—20 sec exercise samples;
6—20 sec recovery samples (first 2 min of recovery);
13— 1 min recoverg samples.

The samples of expired air were analyzed using a Beckman E-2 oxygen analyzer and LB-1, CO_2 analyzer. These instruments were calibrated before each experiment using commercially prepared gas mixtures which were checked using the Haldane apperatus and technique. During the recovery period (between 3 and 5 min), a stool with a foam cushion was slipped over the bicycle seat to insure added comfort.

V_{O_2} Max Test. Maximal oxygen uptake was determined on a progressive workload increment test on the bicycle ergometer. Subjects pedalled at a relatively constant rate of 60 rpm paced by an auditory-visual metranome with a starting friction load of 900 kpm/min. Every 2 min thereafter the frictional resistance was increased 120 kpm/min until the subject stopped pedalling.

Prior to the start of each test, the subjects practiced pedalling at 540 kpm/min in order to become accustomed to the pace. Each subject was encouraged to pedal for as long as possible. Strong vocal encouragement was given throughout the test with the intent of pushing the subject to attain his highest work output.

Minute-by-minute oxygen uptake was measured simultaneously during each minute of ergometer work by the method described earlier. V_{O_2} max was chosen as the highest value in the series of oxygen scores on each individual.

Results and Discussion

Performance and Metabolic Measures. The total number of pedal revolutions turned for the 35 subjects was 85.0 (SD = 7.5). When this value is multiplied by the work per pedal revolution 34.0 kp (5.5 kg × gear ratio of 6), it equals 2890.0 kpm (SD = 255.0). The percent decrement in work-rate from the initial rate is 59.7%.

Table 1. Means and standard deviations for performance and metabolic measures[a]

Variable	Mean	SD
1. Total work (kpm)	2890.0	255.0
2. Resting O_2 income (l/min)	0.32	0.04
3. Peak net exercise O_2 income (l/min)	2.03	0.46
4. Total O_2 income (liters)	2.35	0.46
5. Exercise Ve BTPS (liters)	130.5	34.2
6. Net recovery O_2 (liters)	4.89	1.12
7. Net recovery O_2/kg (ml/kg)	0.068	0.016
8. Gross recovery O_2 (liters)	9.71	1.19
9. Net O_2 deficit (liters)	1.31	0.47
10. Net O_2 deficiency (liters)	3.58	1.69
11. Net O_2 cost of work — O_2 income + O_2 recovery (liters)	6.93	1.42
12. Net work efficiency (percent)	19.3	3.3
13. Gross work efficiency (percent)	11.1	3.7
14. V_{O_2} Max (l/min)	3.34	0.62
15. *Ve* Max (liters)	151.7	17.4

[a] All values are for one-minute performance tests except V_{O_2} max and *Ve* max which were obtained on the increment bicycle test.

Since only one test was administered to each subject, the extent of performance reliability and individual differences cannot be quantified. However, in two separate experiments with a comparable work-rate and number of subjects, the writer has found high test-retest performance reliability, namely $r = 0.89$ and $r = 0.93$ (unpublished observations).

Table 1 gives the means and standard deviations for the observed and calculated metabolic measures during the one-minute test in addition to the V_{O_2} max and max *Ve* obtained during the increment test. The differences between V_{O_2} max and the total O_2 uptake during the one-minute test is 0.99 l ($t = 0.55$, $p > 0.05$) while the difference between max *Ve* measured on the increment test and on the one-minute test is 21.2 l ($t = 7.1$, $p < 0.01$).

Curve Analysis. The close agreement of the theoretical curve with the experimentally determined points shown in the main part of Fig. 1 is convincing; the theoretical formula $Y = ae^{-kt} + C$ for the O_2 income and $Y = a_1e^{-k_1t} + a_2e^{-k_2t} - C$ for the O_2 recovery describes the results very satisfactorily. Evidently, even under conditions where the current O_2 income is inadequate (probably limited by such factors as blood supply), the rate pattern of O_2 uptake is adequately described by the conventional exponential model. It should be noted that this analysis only accounts for the time pattern of O_2 uptake and recovery and does

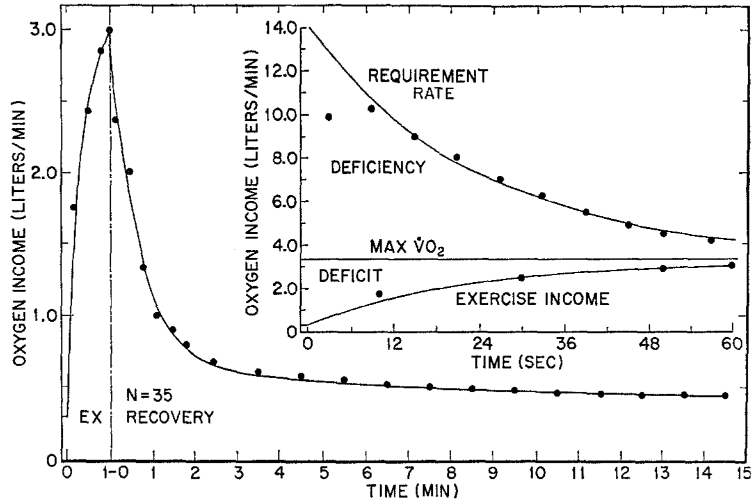

Fig. 1. Exponential oxygen uptake and recovery curves for one-minute supramaximal exercise. See text for calculation of requirement rate, deficiency and deficit shown in the insert figure

not attempt to explain or account for the time pattern of blood lactate accumulation and disappearance, or of biochemical energy production.

Note that V_{O_2} max necessarily represents the asymptotic parameter C of the O_2 uptake curve. The other curve parameters are $a = 3.04$ and $k = 2.256$. The last plotted value is not an observed point but rather corresponds to the computed value at the end of exercise and beginning of recovery. The computed half time for the exercise O_2 uptake is 18.4 sec which is similar to the value previously reported for isolated dog gastrocnemius [27], and for human subjects during the transition from mild to heavy work [8]. This corresponds to an O_2 debt accumulation of 18.9 ml/kg·min for the present exercise which is larger than previously reported [8]. Since the exercise lasted one-minute and only three twenty-second O_2 samples were taken, the fitting of the curve is limited to a one-component analysis. It should be realized that if the exercise had continued for several additional minutes two components might have emerged as it did in the experiments by Henry [9], Henry and DeMoor [14], DeMoor [7], Knuttgen [20], and Royce [28]. The exercise k is roughly $1^1/_2$ times greater than k_1 of recovery.

The recovery curve gives the rate of O_2 uptake Y at any time t in excess of the resting rate established near the end of the recovery period. The terms $a_1e^{-k_1t}$ and $a_2^{-k_2t}$ are the fast and slow components of the recovery oxygen uptake. The measured net O_2 uptake for the 15 min recovery, using the pre-exercise resting level of 0.32 l/min as a reference, is 4.89 l. This is considerably smaller than the observed values of several investigators [6, 16, 25] who reported data for heavy exercise, but similar to the estimate of Margaria *et al.* [24]. The value computed from the 2-component exponential equation using the obtained parameters for the smooth curve: $a_1 = 2.80$, $a_2 = 0.338$, $k_1 = 1.443$, $k_2 = 0.059$, and $C = 0.30$ is 4.67 l or 4.5% less than the observed O_2 recovery. It should be noted that the agreement would be closer if adjustment were made to recognize that this mathematical payoff curve starts about 5 to 10 sec at the official end of exercise. The k's of this equation correspond to half-times of 28.8 sec for the fast component and 11.76 min for the slow component. Table 2 shows a comparison of these curve parameters with other data. Where only $t_{1/2}$ was reported, the k constant was calculated. The measured value of k is computed from the relationship $k = 0.693/t_{1/2}$, where $t_{1/2}$ represents the amount of time required for O_2 to progress from the initial value to one-half the amount of that value. The naperian log base $e = 0.693$.

The average fast component of recovery ($a_1 e^{-k_1 t}$) is 1.44 l or 21 ml/kg-body weight. This is nearly identical to the estimated value based on blood lactate measures of Margaria *et al.* [24], but well under the maximum limit estimated to be 3 or 4 l by Margaria and Edwards in 1934 [25]. However, the actual limit of the fast component is uncertain since the extent of individual differences has not been investigated. The fast component velocity constant (k_1) of 1.58 appears to be within the range reported by others for much lighter work (Table 1). According to Berg [2], this fast velocity constant, k_1, is independent of workload within fairly wide limits; however, the data of Henry and DeMoor [14] shows that it becomes appreciably faster when there is a large increase in the rate of work.

In the case of the slow component of recovery, $a_2 e^{-k_2 t}$, the integral of the curve for 15 min recovery ($a_2/k_2 - a_{15}/k_2$, where $a_2 = 0.338$ and $a_{15} = 0.145$) is 3.27 l which is similar to the 3.0 l estimate of Margaria *et al.* from lactate measurements [24]. The proportion of slow component recovery to total recovery is roughly 69%. To determine precisely the magnitude of the recovery constant it is necessary to follow recovery for 1 to 2 h. This necessitates that subjects remain relaxed and quiet as they approach their asymptotic resting values. It was not possible to observe these requirements in the present study. The effect of a shortened recovery time is to increase the magnitude of the k_2 constant resulting in an apparent slow component that is smaller than the true values. Since the integral for the slow component becomes a_2/k_2 at infinity, the calculated value of Y at the asymptote C yields an additional

Table 2. Comparison of total recovery O_2, and exponential curve parameters

Study	Exercise	Recovery time min	Total rec. O_2 l	Fast component $t_{1/2}$ sec	k_1	Slow component $t_{1/2}$ min	k_2
Present study $N = 35$ ♂	Bicycle — 2890 kpm in 1 min	15	4.89	28.8	1.443	11.76	0.059
Hill (1924) $N = 1$ ♂	Running — 2.86 to 4.7 m/sec for 2 to 4 min	160	4.0—18.6	24.0—37.8	1.10—1.73	—	—
Margaria *et al.* (1933) $N = 1$ ♂	Treadmill — varying grades 14 km/h	110	~ 7.3	25.02—39.96	1.04—1.66	34.65	0.02
Berg (1947) $N = 28$ ♂	Step test — 9 inch and 20 steps/min for 3 min	—	~ 1.0	31.3	1.330	—	—
Henry and DeMoor (1950) $N = 9$ ♀	Bicycle a) 690 kpm/min — 6 min b) 920 kpm/min — 6 min	35	a) 2.52 b) 4.45	a) 39.2 b) 37.6	1.059 1.107	5.5 4.8	0.125 0.144
Henry and Berg (1950) $N = 23$ ♂	Step test — 9 inch and 20 steps/min for 4 min	—	11.5 ml/kg	29.65 27.30	1.40 1.52	—	—
Henry *et al.* (1951) a) $N = 35$ ♂ b) $N = 25$ ♂	Bicycle a) 620 kpm/min (69 rpm) 6 min b) 95 kpm/min (116 rpm) 6 min	a) 25 b) 25	a) 1.18 b) 1.18	a) 44.9 b) 48.2	0.925 0.863	—	—
DeMoor (1954) $N = 22$ ♂ 21 ♀	Bicycle — 680 kpm for 6 min 62 rpm	25	2.60	36.7	1.132	3.92	0.177
Henry and DeMoor (1956) $N = 43$	Bicycle — 680 kpm/min for 6 min	25	2.46	43.2	0.962	4.1	0.169
Royce (1969) $N = 13$ ♂	Bicycle — 2/3 max load 4 to 7.5 min — 50 rpm	18	5.20	54.2	0.766	16.50	0.042
Katch *et al.* (1972) $N = 50$ ♂	Bicycle 1656 kpm/min for 12 min (69 rpm)	10	5.60	27.4	1.518	10.2	0.068

0.94 l. This would result in a total net O_2 recovery of 5.83 l which is similar to the maximal value for surplus O_2 during recovery reported by Welch *et al.* on their one subject [32].

The insert of Fig. 1 was constructed in order to examine the data with respect to the concept that for an extended period of time, supramaximal work (work requiring a greater O_2 consumption that can be supplied by the aerobic power) decreases exponentially per-unit time approaching a level that can be maintained by the aerobic power. Shown are the curves for the O_2 requirement-rate and O_2 income during the exercise. V_{O_2} max is shown as the horizontal line. The oxygen requirement-rate values are calculated as follows: The minute-by-minute work (kpm/min) is converted to equivalent by dividing the work by 2153 kpm (1 l $O_2 = 2153$ kpm) then dividing the O_2 equivalent by the calculated efficiency (in this case 19.34%, Table 1). For the total O_2 requirement, for example, the O_2 equivalent (1.342 l) is 2.890 kpm divided by 2153 kpm. This equivalent divided by the efficiency (0.1934) constitutes a requirement of 6.93 l. These calculations are based on the assumption that the efficiency remains constant throughout work and recovery. It is possible that this assumption is not true; however, this should not change the basic analysis since the curve would approach the same asymptote (V_{O_2} max) but only at a different rate. The term *deficiency* is used here to denote the difference between the V_{O_2} max and O_2 requirement-rate. This should not be confused with the *deficit*, which is defined as the difference between the amount of O_2 consumed and the O_2 uptake that would have been, had the uptake reached a steady level instantaneously. During the submaximal exercise there is no deficiency, only a deficit. The deficit plus the deficiency have often been combined and called the deficit, but when it is possible to calculate a requirement-rate curve determining the deficiency is helpful in analyzing the total oxygen debt.

The mathematical curve $Y = ae^{-kt} - C$ was used to fit the smooth curve to the calculated requirement-rate values. The curve parameters are $a = 10.80$, $k = 2.349$ and $C = 3.34$ (V_{O_2} max). The fact that this curve declines at the very instant the subject begins pedalling probably reflects the fact that physiological fatigue begins with the inititation of movement. For the present purposes, this can be considered in broad terms resulting from a decline in the biochemical release of energy, or from the accumulation of metabolites that decrease muscle energy. The net effect of this fatigue is to reduce work output per-unit time. This situation is described quite well by the above mathematical expression.

It should be noted that the curve parameter a of this requirement-rate equation theoretically represents the maximal amount of energy supply in O_2 units available at the very beginning of exercise. This is equal to 14.14 l, or 70.7 kcal which is well within the range predicted by Margaria *et al.* [23] for the alactiacid O_2 capacity. The fact that the first observed value is off the curve probably reflects the necessity for overcoming inertial factors, and complications caused by the sudden increase in the friction load on the flywheel.

The requirement-rate curve and O_2 uptake curve have a common asymptote, V_{O_2} max; they also have similar half-times, for the requirement rate $t^1/_2$ is 17.5 sec and for the O_2 income curve it is 18.4 sec. It is a simple matter to calculate the time when these two curves approach a certain percentage of the asymptotic parameter C; in 1 min the two curves are 10% from the asymptote, 5% in 78 sec, and 1% in 2 min. This indicates that using this work profile the subjects would have reached their V_{O_2} max in approximately 2 min.

Since continuation of the work beyond the 1 min would have eventually resulted in a steady state O_2 uptake equal to the V_{O_2} max, when calculating the deficit according to standard methods [33] this steady state value must be used. In this case, the deficit equals 1.31 l. The surplus O_2 during recovery is 73% greater than this deficit, while the deficiency (3.58 l) plus the deficit is identical with the recovery O_2 uptake (Table 1).

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