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Slow upward drift of $\dot{V}_{O_2}$ during constant-load cycling in untrained subjects

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Summary. The oxygen uptake kinetics during constant-load exercise when sitting on a bicycle ergometer were determined in 7 untrained subjects by measuring breath-by-breath $\dot{V}_{O_2}$ during continuous exercise to volitional exhaustion (mean endurance time $= 1160 \pm 172$ s) at a pedal frequency of 70 revolutions $\cdot$ min^{-1}. The power output, averaging 189.5 W, was set at 82.5% of that eliciting the individual $\dot{V}_{O_{2\,max}}$ during a 5 min incremental exercise test. Throughout the exercise period, the $\dot{V}_{O_2}$ kinetics could be appropriately described by a two-component exponential equation of the form:

$$\dot{V}_{O_2}(t) = Y_a[1-\exp(-k_a t)] + Y_b[1-\exp(-k_b t)]$$

where $\dot{V}_{O_2}$ is net oxygen consumption and t the time from work onset. $\dot{V}_{O_2}$ measured at the end of exercise was close to $\dot{V}_{O_{2\,max}}$ (98% $\dot{V}_{O_{2\,max}}$) and the mean values of Y_a, k_a, Y_b and k_b amounted to 1195 ml $O_2 \cdot$ min^{-1}, 0.034 s^{-1}, 1562 ml $O_2 \cdot$ min^{-1}, and 0.005 s^{-1} respectively. The initial rate of increase in $\dot{V}_{O_2}$ predicted from the above equation is slower than that calculated, for the same work intensity, on the basis of the data obtained by Morton (1985) in trained subjects. For $t > 480$ s, however, the two models yield substantially equal results.

Key words: Oxygen uptake kinetics — Constant-load exercise

Introduction

After the start of constant-load bicycle ergometer exercise requiring less than 60% $\dot{V}_{O_{2\,max}}$, oxygen consumption increases to a steady level within a short period of time (Bason et al. 1973). According to several authors (Whipp an Wasserman 1972; Nagle et al. 1970; Hagberg et al. 1978), however, the time to steady state is prolonged at work rates requiring more than 60% $\dot{V}_{O_{2\,max}}$. At these high work rates, the oxygen uptake curve can be described by a two-component model (Whipp and Wasserman 1972) or by a double exponential (Bason et al. 1973), the slower component becoming apparent only if the exercise duration is long enough (more than 3 min) (Whipp and Wasserman 1972).

The majority of data dealing with the effects of exercise intensity on oxygen uptake kinetics were obtained in a range of exercise intensities from 60 to 80% $\dot{V}_{O_{2\,max}}$ (Hagberg et al. 1978; Whipp and Wasserman 1972; Bason et al. 1973). To our knowledge, the maximal amplitude of the slow increase of $\dot{V}_{O_2}$ during moderately high intensity ergometer exercise has never been measured, since in previous studies the exercises were not systematically performed until exhaustion. The aim of this study was to evaluate the maximal upward drift of $\dot{V}_{O_2}$ to the end of submaximal cycling exercise performed until volitional exhaustion by untrained subjects.

Experimental procedure, methods and calculations

The experiments were performed by seven subjects whose mean physical characteristics are reported in Table 1. $\dot{V}_{O_{2\,max}}$ was measured by an open-circuit method during continuous exercise on a bicycle ergometer at 70 rpm. The initial work rate of the exercise was 100 W and was increased by 50 W every 5 min until exhaustion. Expired air was collected during the last min of each work stage in two air tight rubber balloons, and the composition of the gas was determined as soon as possible after collection by means of previously calibrated O_2 and

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Table 1. Mean values (X) and standard deviations (SD) of the main physical characteristics of the subjects

Subjects	Body weight (kg)	Age (years)	$\dot{V}_{O_{2max}}$ ($l \cdot min^{-1}$)
1	79	51	2.98
2	71	43	3.15
3	51	29	3.10
4	82	30	3.86
5	72	40	3.59
6	73	32	3.32
7	69	29	2.86
M	71	36	3.26
SD	9.94	8.5	0.36

CO_2 analyzers. The expired volumes were measured by means of a dry gas meter. $\dot{V}_{O_{2max}}$ was assumed to be attained when a subsequent power increment did not elicit any substantial increase in $\dot{V}_{O_2}$. The relationship between $\dot{V}_{O_2}$ measured at the end of each work rate (steady state $\dot{V}_{O_2}$, $\dot{V}_{O_{2ss}}$) and mechanical power (P) was established from these measurements for each subject. The individual relationships were found to be linear until $\dot{V}_{O_{2max}}$; they were used to calculate the mechanical power values corresponding to 80 and 85% $\dot{V}_{O_{2max}}$ (P_{80} and P_{85}).

In subsequent sessions, the subjects exercised at either of these two work rates until volitional exhaustion (temps-limite, t_{lim}, Scherrer and Monod 1960), defined as the moment at which the predetermined frequency of 70 r.p.m. could no longer be maintained. Each exercise period was preceded by 5 min rest in a sitting position on the bicycle. O_2 uptake was determined on a breath-by-breath basis at rest and throughout the overall exercise period. The method used in this study was developed and described by Giezendanner et al. (1983): it allows alveolar gas exchange to be determined by taking into account the variation in the amount of gas stored in the lungs. The pedalling frequency was established during a brief period of loadless pedalling, and was controlled visually by means of a frequency counter displaying the number of revolutions per min. When the pedal frequency attained 70 r.p.m., the resistance was fixed, this instant being considered as the onset of exercise. This procedure was used to avoid the inertia of the still flywheel. The amplitude of the slow upward drift of oxygen uptake ($\Delta\dot{V}_{O_2}$) was calculated by substracting the $\dot{V}_{O_{2ss}}$ corresponding to the mechanical power developed (as established in the previous series of experiments), from the $\dot{V}_{O_2}$ measured at the end of the exhausting exercises.

The oxygen uptake kinetics were characterized by drawing smooth curves by eye through the single breath $\dot{V}_{O_2}$ points, as described by di Prampero et al. (1983). It was postulated that the general form of the equation representing the function $\dot{V}_{O_2}=f(t)$ was similar to that described by Bason et al. (1973):

$$\dot{V}_{O_2}(t) = Y_a[1-\exp(-k_a t)] + Y_b[1-\exp(-k_b t)] \quad (1)$$

where $\dot{V}_{O_2}(t)$ is the rate of O_2 uptake at time t ($ml\ O_2 \cdot min^{-1}$), t is expressed in s, Y_a and Y_b are the amplitudes of the fast and slow components, and k_a and k_b the corresponding velocity constants. These are related to the time required to rach 50% of the corresponding amplitudes (t ½) by the following equation:

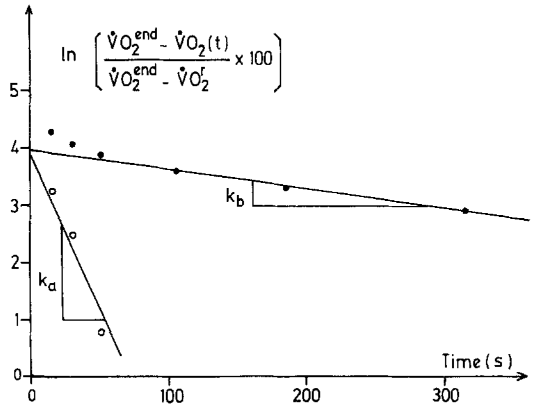

Fig. 1. Graphic analysis of the $\dot{V}_{O_2}$ uptake kinetics in 1 subject. $\dot{V}_{O_{2end}}$, $\dot{V}_{O_2,t}$, and $\dot{V}_{O_2,r}$ indicate the O_2 consumption at end of exercise (exhaustion), at time t and at rest before work onset respectively. See text for further details

$$k_a = \frac{\ln(2)}{t\,½_a}; \quad k_b = \frac{\ln(2)}{t\,½b} \quad (2)$$

A limited number of points were then selected on the curves fitted by eye, and the parameters of equation (1) determined by plotting the logarithm of the difference between the $\dot{V}_{O_2}$ at the end of exercise ($\dot{V}_{O_{2end}}$) and $\dot{V}_{O_2}(t)$, normalized for the net $\dot{V}_{O_{2end}}$ ($\dot{V}_{O_{2end}}$ minus $\dot{V}_{O_{2rest}}$), as a function of the time elapsed from work onset (see Fig. 1) (as the time delay required to attain the pedal frequency of 70 r.p.m. was short (3–7 s), the $\dot{V}_{O_2}$ increase during loadless pedalling was neglected).

As shown in Fig. 1, a straight line was then drawn through the points for $t > 120$ s, in this case, the three points on the right. The criterion used to select these points was that, in general, the data for $t > 120$ s could be satisfactorily interpolated by a straight line regression, when plotted as in Fig. 1. The intercept of this line with the Y-axis is equal to $\ln Y_b$, where Y_b is expressed as a percentage of $\dot{V}_{O_{2end}}$, and the rate constant of the slow component (k_b, in s^{-1}) is given by the slope of this line. The fast component was then obtained by subtracting from the measured total $\dot{V}_{O_2}$ the absolute amount of $\dot{V}_{O_2}$ ($ml \cdot min^{-1}$) due to the slow component, as obtained by back extrapolation. The logarithm of this difference was then plotted as a function of time (open dots in Fig. 1). A straight line interpolation through these points yielded $\ln Y_a$ (where Y_a is the amplitude of the fast component expressed as a percentage of $\dot{V}_{O_{2end}}$), and k_a. Obviously enough this procedure is based on the assumptions that, for $t > 120$ s, $\dot{V}_{O_2}$ due to the fast component is negligible, and that $\dot{V}_{O_{2end}} = Y_a + Y_b$.

Results

The main physical characteristics of our subjects are listed in Table 1 (mean values ±1 SD). Their average $\dot{V}_{O_{2max}}$ measured during the course of incremental exercise by an open circuit method was $3.26 \pm 0.36\ l \cdot min^{-1}$ (mean value ±1 SD).

Mean t_{lim} was equal to 1160 s, with a fairly large dispersion (range: 480 to 2400 s).

The breath-by-breath time course of $\dot{V}_{O_2}$ up-

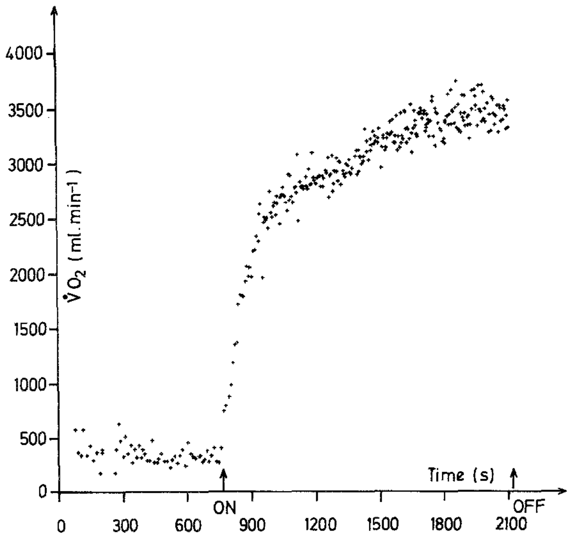

Fig. 2. Plot of an individual single breath data points for $\dot{V}_{O_2}$ during the course of constant-load exercise (subject n°6, mechanical power: 217 W, P_{85})

take during constant-load exercise is shown in Fig. 2 for 1 subject at 1 work load. In all cases, $\dot{V}_{O_2}$ increased rapidly to about 80% $\dot{V}_{O_{2end}}$, the $\dot{V}_{O_2}$ rise becoming appreciably slower after about 2.5 min from work onset. The individual results of this type of graphical analysis (see above and Figs. 1 and 2), at both work rates (P_{80} and P_{85}) are reported in Table 2. Only k_a was significantly different in the two intensity classes (unpaired t test, $p<0.05$). If this difference is disregarded, the $\dot{V}_{O_2}$ response curve can be described by a general equation where the different parameters are the mean values of Y_a, Y_b, k_a and k_b calculated by pooling all data together.

The resulting equation is described by:

$$\dot{V}_{O_2}(t)=41.9[1-\exp(-0.034\ t)] + 54.8[1-\exp(-0.005\ t)] \quad (3)$$

where $\dot{V}_{O_2}(t)$ is expressed as percent of $\dot{V}_{O_{2end}}$ and t is s. Since mean $\dot{V}_{O_{2end}}$ was 2851 ml $O_2 \cdot min^{-1}$ above resting, the net $\dot{V}_{O_2}$ time course ($\dot{V}_{O_2}$ in ml $O_2 \cdot min^{-1}$) is described by:

$$\dot{V}_{O_2}(t)=1195[1-\exp(-0.034\ t)] + 1562[1-\exp(-0.005\ t)] \quad (4)$$

where the sum of the amplitudes Ya and Yb ($=1195+1562=2757$) is fairly close to the measured $\dot{V}_{O_{2end}}$, and not far from the subjects $\dot{V}_{O_{2max}}$. The $\dot{V}_{O_2}$ kinetics predicted from equation 3 are represented in Fig. 3, curve 1. Curves 2 and 3 were obtained by assigning to the constants of eqn (3) the average values plus, or minus, 1 standard error of the mean (Table 2).

The oxygen uptake kinetics during short term bicycle ergometer exercise in trained subjects was described by Morton (1985) taking into account both the time after the work onset and the mechanical power (P):

$$\dot{V}_{O_2}=0.0012\ Pt+1.821\ P[1-\exp(-0.031\ t)] \quad (5)$$

where $\dot{V}_{O_2}$ is expressed in $l \cdot min^{-1}$, P in thousands of kpm and t in s. In order to compare the

Table 2. Mean values (X) of individual results of graphic analysis of the O_2 uptake kinetics during constant load exercise. Standard error of the mean is also indicated

Subjects	Mechanical work		Y_a	k_a (s^{-1})	Y_b	k_b (s^{-1})	$\dot{V}_{O_{2end}}$ ml $O_2 \cdot min^{-1}$	t_{lim} (s)
	Power (W)	Rate						
1	182	$P80$	44.7	0.038	49.4	0.004	3290	750
1	189	$P85$	49.4	0.031	49.0	0.004	3240	840
2	182	$P80$	49.0	0.055	51.0	0.003	3340	905
2	189	$P85$	28.5	0.045	70.1	0.005	3250	773
3	168	$P80$	59.0	0.030	41.0	0.005	2250	2400
3	175	$P85$	49.6	0.044	47.0	0.004	2900	1612
4	217	$P80$	33.1	0.018	57.4	0.008	3700	2100
4	224	$P85$	38.5	0.046	57.0	0.006	3530	975
5	210	$P80$	40.4	0.022	58.0	0.007	3100	1817
6	210	$P80$	49.0	0.020	42.5	0.003	4000	1196
6	217	$P85$	49.0	0.033	54.0	0.005	3420	673
7	147	$P80$	27.1	0.040	70.0	0.004	2720	600
7	154	$P85$	27.0	0.023	66.7	0.005	2600	480
X	189.5	82	41.9	0.034	54.8	0.005	3180	1160.8
SEM	6.9	0.7	2.8	0.003	2.5	0.0003	130.6	172.2

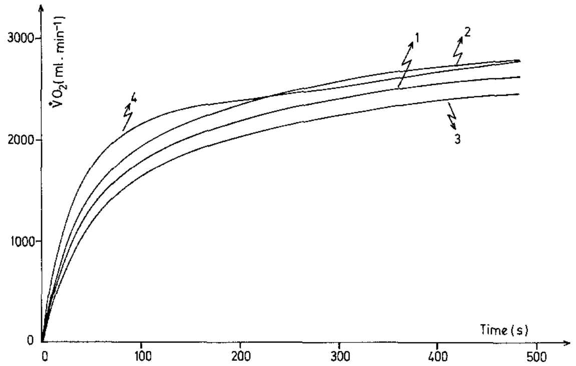

Fig. 3. Time course of net oxygen uptake during constant-load exercise. Curve 1 is drawn by solving equation (3). Curves 2 and 3 are obtained by adding and substracting 1 SEM from the mean value of the parameters of equation (3). Curve 4 is drawn by solving Morton's equation *(equation 5)* for work intensity equal to the average of the present data

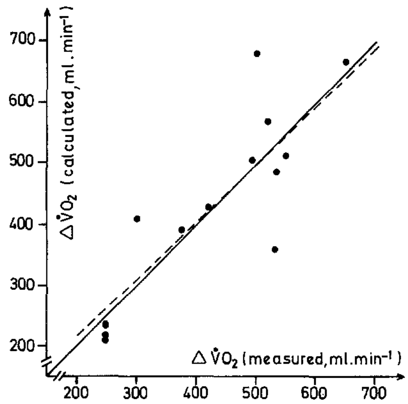

Fig. 4. Relationship between calculated $\Delta\dot{V}_{O_2}$ obtained by solving equation (6) and measured $\Delta\dot{V}_{O_2}$. The full line is the bisectrix of the axis. The interrupted line is drawn by solving the regression equation characterizing the relationship between calculated $\Delta\dot{V}_{O_2}$ and measured $\Delta\dot{V}_{O_2}$: calculated $\Delta\dot{V}_{O_2}=22.61+0.965$ measured $\Delta\dot{V}_{O_2}$ ($r=0.842$; $p<0.001$)

oxygen uptake kinetics of our subjects with Morton's model (1985), curve 4 was drawn in Fig. 3 by solving Morton's equation for a power output corresponding to the average in our experiments (189.5 W).

As shown in Fig. 3, the early increase in $\dot{V}_{O_2}$ as a function of time occurs more rapidly in the trained subjects, but the $\dot{V}_{O_2}$ calculated after 480 s of exercise does not seem to differ significantly from the $\dot{V}_{O_2}$ calculated from the present data. This observation seems to indicate that, at the same work rate, the oxygen transport system and/or the oxygen-extraction processes by skeletal muscles are more efficient in trained subjects. The slope of curve 4 also suggests that the rate of the slow component of $\dot{V}_{O_2}$ increase is slowed by some adaptation induced by training.

The amplitude of the slow upward drift of O_2 uptake ($\Delta\dot{V}_{O_2}$), calculated by subtracting the $\dot{V}_{O_2}$ measured during a 4.5 min exercise from $\dot{V}_{O_{2end}}$ at P 82.5 amounted on average to 440.3 ± 42.9 ml $O_2\cdot min^{-1}$ (mean ±1 SEM). This is close to the value that can be calculated by substracting from Y_b (1562 ml $O_2\cdot min^{-1}$) the $\dot{V}_{O_2}$ value obtained when solving the slow component equation of the $\dot{V}_{O_2}$ kinetics for $t=270$ s, i.e., the duration of the exercise during which the "steady state" $\dot{V}_{O_2}$ was actually determined:

$$\dot{V}_{O_2}=1562-1562[1-\exp(-0.005\times270)] \\ =405 \text{ ml } O_2\cdot min^{-1} \quad (6)$$

The agreement between the values obtained above supports the view that the slow component of the $\dot{V}_{O_2}$ kinetics was indeed correctly estimated. This conclusion is also supported by the fact that the relationship between the calculated $\Delta\dot{V}_{O_2}$ obtained by solving equation (6) for each subject and measured $\Delta\dot{V}_{O_2}$ is highly significant ($r=0.842$; $p<0.001$). This relationship is illustrated by Fig. 4.

Discussion

The endurance time (mean t_{lim}) in our subjects, averaged for both work rates (P_{80} and P_{85}), was 1160 s. This figure is consistent with previous observations (Camus et al. 1980), where eight healthy young men were running as long as possible on a motor-driven treadmill at comparable work rates. It is also consistent with the theoretical value of t_{lim} obtained by solving the empirical equation described by Grosse-Lordemann and Müller (1937).

Consistent with the results obtained by several authors (Whipp and Wassermann 1972; Hagberg et al. 1978; Bason et al. 1973) the semilogarithmic plot of the net $\dot{V}_{O_2}$ time course clearly shows that the oxygen uptake kinetics during constant-load exercise can be described by a two-component exponential model. The type of graphical analysis described above should be taken with some caution in view of the subjectivity implied in the interpolation of the data points by eye. However, when the same set of results were analysed independently by two investigators, the results obtained, in terms of the four constants of equation (1), were essentially the same.

As can be seen in Table 2, the scatter of t_{lim}

data is fairly large, an observation which depends presumably on the fact that the physical characteristics of our subjects differed fairly widely.

Even if these experiments do not give any specific information on the factors that set t_{lim}, it is noteworthy that in our subjects, $\dot{V}_{O_{2end}}$ was close to $\dot{V}_{O_{2max}}$ whatever the maximum duration of exercise.

The role played by central and peripheral factors in setting oxyen uptake kinetics during exercise is still a matter of debate among physiologists. According to Pendergast et al. (1980), the t ½ of the $\dot{V}_{O_2}$ response at the onset of muscular exercise is limited by O_2 utilization by skeletal muscles. This hypothesis-supported by the observation that the t ½ of $\dot{V}_{O_2}$ kinetics is significantly slower than that of cardiac output and muscle blood flow- is contrary to conclusions arrived at by Hughson and Morrissey (1983), who maintain that the rate of adaptation of the O_2 transport system is the main limiting factor. The results of the present observation do not shed light on this controversy. It must be kept in mind, however, that the t ½ of the fast component (20 s) is close to the t ½ of cardiac output in transition from rest to mild exercise in untrained subjects (Davies et al. 1972). This observation suggests that the rapid increase in $\dot{V}_{O_2}$ is closely linked with the adaptation of the cardiac output at the onset of exercise.

The finding that $\dot{V}_{O_2}$ keeps increasing, albeit at a slower rate, up to the end of constant-load exercise is in agreement with the results reported by several authors (Whipp and Wasserman 1972; Bason et al. 1973; Hagberg et al. 1978). Despite the wide number of studies on this topic, the origin of the slow rise of $\dot{V}_{O_2}$ remains obscure. Several hypotheses were proposed to explain this phenomenon. According to Henry (1951), this rise is due to the removal of the lactate which appears in the blood during exercise. On the contrary, according to Hagberg et al. (1978), the slow rise of $\dot{V}_{O_2}$ at 80% $\dot{V}_{O_{2max}}$ is due entirely to the increase in temperature and ventilation.

Other factors could also be held responsible for the gradual rise in $\dot{V}_{O_2}$. It has been shown in fact that when the intensity of exercise reaches 80–90% $\dot{V}_{O_{2max}}$, fast-twitch motor units are also recruited, leading to lactic acid production in skeletal muscles. The intramuscular acidosis resulting from the dissociation of lactic acid seems to be directly involved in the loss of force exerted by muscle fibers (Hermansen 1981). As a consequence, some fast-twitch motor units are newly recruited in order to compensate the loss of force exerted by the fatigued motor units. Such a recruitment pattern has been shown to occur in several species including man (Gollnick et al. 1973). This recruitment of new fibres would cause cardiac output and $\dot{V}_{O_2}$ to increase continuously, providing that the fatigued fibres recruited at first continue to be stimulated and consume oxygen despite a reduction in force production.

The continuous slow increase in $\dot{V}_{O_2}$ after the first 2–3 min of exercise could also be due to a continuous drift of free creatine (Cr) concentration in working muscle as a consequence of lactic acid production by fast fibres. Indeed, the equilibrium of Lohmann's reaction ($ADP + PC \longleftrightarrow ATP + Cr$; $K = (ATP \times Cr)/(ADP \times PC)$ is displaced to the right at low pH (Harris et al. 1977). This leads to an increase in the concentration of free creatine in skeletal muscle, which may in turn be considered as the "signal" bringing about an increased oxygen consumption by skeletal muscles (Mahler 1980; di Prampero 1984; di Prampero and Margaria 1968).

In conclusion, it appears that several mechanisms could be responsible for the continuous rise of $\dot{V}_{O_2}$ during exercise. However, their relative role in setting the slow component of the $\dot{V}_{O_2}$ response curve remains to be determined quantitatively.

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