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Oxygen uptake as related to work rate increment during cycle ergometer exercise

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Summary. We postulated that the commonly observed constant linear relationship between $\dot{V}_{O_2}$ and work rate during cycle ergometry to exhaustion is fortuitous and not due to an unchanging cost of external work. Therefore we measured $\dot{V}_{O_2}$ continuously in 10 healthy men during such exercise while varying the rate of work incrementation and analyzed by linear regression techniques the relationship between $\dot{V}_{O_2}$ and work rate ($\Delta\dot{V}_{O_2}/\Delta$wr). After excluding the first and last portions of each test we found the mean $\pm$SD of the $\Delta\dot{V}_{O_2}/\Delta$wr in $ml \cdot min^{-1} \cdot W^{-1}$ to be 11.2 ± 0.15, 10.2 ± 0.16, and 8.8 ± 0.15 for the 15, 30, and 60 $W \cdot min^{-1}$ tests, respectively, expressed as $ml \cdot J^{-1}$ the values were 0.187 ± 0.0025, 0.170 ± 0.0027 and 0.147 ± 0.0025. The slopes of the lower halves of the 15 and 30 $W \cdot min^{-1}$ tests were 9.9 ± 0.2 $ml \cdot min^{-1} \cdot W^{-1}$ similar to the values for aerobic work reported by others. However the upper halves of the 15, 30, and 60 $W \cdot min^{-1}$ tests demonstrated significant differences: 12.4 ± 0.36 vs 10.5 ± 0.31 vs 8.7 ± 0.23 $ml \cdot min^{-1} \cdot W^{-1}$ respectively. We postulate that these systematic differences are due to two opposing influences: 1) the fraction of energy from anaerobic sources is larger in the brief 60 $W \cdot min^{-1}$ tests and 2) the increased energy requirement per W of heavy work is evident especially in the long 15 $W \cdot min^{-1}$ tests.

Key words: Lactate — Maximum oxygen uptake — Oxygen uptake kinetics — Work efficiency

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Introduction

There is good evidence to suggest that the O_2 cost of aerobic cycle ergometry approximates 10.0 to 10.5 $ml \cdot min^{-1} \cdot W^{-1}$ (Gaesser and Brooks 1975; Wasserman and Whipp 1975; Spiro 1977) corresponding to a work efficiency of 27% (Pahud et al. 1980). Many investigators, using several-minute periods of constant cycle ergometry work over a wide range of intensities, have reported a linear relationship between the work rate and the resultant "steady-state" O_2 uptake ($\dot{V}_{O_2}$) (Asmussen 1965; Astrand and Rodahl 1971; Cotes 1975). Others, after excluding the data obtained shortly after the onset of exercise, have found a similar linear relationship during cycle work to exhaustion, whether increment steps lasted a second or a minute or two (Nagle et al. 1971; Wasserman and Whipp 1975; Spiro 1977; Jones and Campbell 1982; Davis et al. 1982).

It is puzzling that a linear increase in work rate appears to elicit a strictly linear response of $\dot{V}_{O_2}$ because exercise at high work rates is not supported solely by atmospheric oxygen but is supplemented energetically by ATP generated by anaerobic metabolism (Keul et al. 1972). We hypothesized that a careful analysis of $\dot{V}_{O_2}$ responses to incremental work would reveal a nonlinear relationship and the pattern of the responses would depend on the magnitude of the incremental work rate. We analyzed the $\dot{V}_{O_2}$ response to exercise using breath-by-breath measurement of gas exchange in 10 healthy young men during cycle ergometry to exhaustion, using different work rate increment protocols.

Materials and methods

Subjects. Ten healthy men volunteered for the study. Their mean ($\pm$SD) age, height, and weight were 22 ± 2.5 years, 177±7.4 cm, and 83±4.9 kg, respectively. They were non-smokers, they had no history or systemic disease and were not engaged in physical training or dietary programmes.

Protocol. Each subject performed 6 tests in random order on 3 different days. They involved work rate increments of 15, 30, and 60 $W \cdot min^{-1}$; duplicates of each test were performed by each subject. The daily tests were separated by 1 to 2 h, test days by 1 to 21 days. In each study, after 4 min of unloaded pedalling at 60 rev. min^{-1} on an electromagnetically braked cycle ergometer (Godart), work rate was increased every 1/2 s at 1 of the 3 rates under computer control (ramp pattern). The increments continued until the subject could no longer maintain pedalling frequency.

Data collection. The subject breathed through a mouthpiece attached to a turbine device (Alpha Technologies) which measured expired and inspired volume continuously. Respired gas was sampled from the mouthpiece at a rate of 60 $ml \cdot min^{-1}$ for continuous measurement of O_2, CO_2 and N_2 by mass spectrometry (Perkin-Elmer MGA 1100). After computer alignment of the gas concentration and volume signals for the transit delay and response time of the mass spectrometer, $\dot{V}_{O_2}$ was computed breath-by-breath as previously described (Beaver et al. 1981). We defined the maximum $\dot{V}_{O_2}$ as the average $\dot{V}_{O_2}$ during the last 10 s of exercise.

Data analysis. The difference between the breath-by-breath $\dot{V}_{O_2}$ and the mean $\dot{V}_{O_2}$ of the last 3 min of unloaded pedalling was calculated and termed the $\Delta\dot{V}_{O_2}$. For each test, we plotted and analyzed the continuous relationship between either time or work rate on the abscissa and the $\Delta\dot{V}_{O_2}$ on the ordinate. For analysis of the $\Delta\dot{V}_{O_2}$ versus work rate relationship ($\Delta\dot{V}_{O_2}/\Delta wr$) which can also be expressed as $\Delta\dot{V}_{O_2} \cdot J^{-1}$ we laterally shifted the data for each test towards zero on the same graph by 45 s. This duration approximates the time constant for $\dot{V}_{O_2}$ increase (Wasserman et al. 1987). This lateral shift is 11.25 W for the 15 $W \cdot min^{-1}$ ramp, 22.5 W for the 30 $W \cdot min^{-1}$ ramp, and 45 W for the 60 $W \cdot min^{-1}$ ramp. (Please see Appendix for rationale and physiologic basis of this shift.)

We used the least squares method of linear regression to analyze the average slope of the $\Delta\dot{V}_{O_2}/\Delta wr$ for each test, excluding the first 100 s and last 15 s of the response for the following reasons: 1) The response of $\dot{V}_{O_2}$ to incremental exercise has been shown to approximate a first order system, so it is predictable that there will be an initial lag in $\Delta\dot{V}_{O_2}$ after the onset of incremental work (Whipp et al. 1981). As the time constant for $\dot{V}_{O_2}$ averages 40—45 s in healthy subjects, over 95% of this lag should be finished by 100 s (one time constant approximates 63% of the expected change while two approximate 95%). 2) In several tests the $\dot{V}_{O_2}$ reached a plateau 10 to 20 s before exercise ended.

Because the $\Delta\dot{V}_{O_2}/\Delta wr$ for each subject was not strictly linear by inspection, we divided the response into two portions (lower and upper) and recalculated the $\Delta\dot{V}_{O_2}/\Delta wr$ over the same time portions of the tests, dividing the portions by the time at which $\dot{V}_{O_2}$ reached half of the distance between unloaded $\dot{V}_{O_2}$ and maximum $\dot{V}_{O_2}$.

We used a paired t-test to compare slopes of the two halves of each exercise test and an analysis of variance with the Tukey test to compare slopes among the three exercise increments. We considered $p<0.05$ significant.

Results

General

We excluded 2 tests of the 60 tests from analyses (one each of the 15 $W \cdot min^{-1}$ increment tests of subjects 6 and 7) because of technical errors and based all calculations on the remaining 58 tests. The unloaded $\dot{V}_{O_2}$ correlated positively with body weight. Among subjects, the maximum $\dot{V}_{O_2}$ did not differ significantly between work rate increments, tests performed on a given day, or during the course of the study. However, the maximum work rate achieved was always highest for the 60 $W \cdot min^{-1}$ work rate increment (Table 1).

Table 1. Comparison of maximum $\dot{V}_{O_2}$, maximum work rate, and duration of exercise for progressively increasing work rate tests of 15, 30, and 60 $W \cdot min^{-1}$ increments

Subject	Maximum $\dot{V}_{O_2}$ ($l \cdot min^{-1}$) Mean±SD	Maximum work rate (W)			Duration (s)		
		Work rate increment ($W \cdot min^{-1}$)					
		15	30	60	15	30	60
1	2.95±0.16	254	269	309	1015	538	309
2	3.45±0.18	251	306	345	1005	613	345
3	3.43±0.19	249	308	328	997	617	328
4	3.14±0.38	250	272	299	1000	545	299
5	3.29±0.18	226	258	297	902	517	297
6	3.10±0.09	209	237	293	835	474	293
7	3.74±0.26	304	351	382	1215	702	382
8	4.00±0.13	296	341	381	1185	682	381
9	3.19±0.09	222	262	305	877	525	305
10	2.82±0.23	190	230	290	760	461	290
Mean±SEM		245*±11	283*±13	322±11	979*±45	567*±26	322±11

* Values are significantly different ($p<0.05$)

Visual analysis

For each subject, $\dot{V}_{O_2}$ (plotted against time): a) rose promptly and stabilized during unloaded pedalling, b) began rising in a curvilinear pattern for the first two minutes of incremental work, c) maintained a relatively linear pattern during the next portion of the test, and d) often deviated from this line in the latter portion of the test. Figure 1 shows the typical pattern of $\Delta\dot{V}_{O_2}$ against time at 3 different work rate increments in a single subject; Fig. 2 shows the same data plotted against work rate.

When the lines of $\Delta\dot{V}_{O_2}$ plotted against work rate were shifted to the left by 45 s to adjust for the approximate time constant for $\dot{V}_{O_2}$ increase, the $\Delta\dot{V}_{O_2}/\Delta$wr plots for the 15 $W \cdot min^{-1}$ increment rate were invariably steepest and for the 60 $W \cdot min^{-1}$ were shallowest for the upper portions of the curves (see Fig. 3). This same systematic pattern was evident for each subject if the plots for the 3 work rate increments were shifted by 30 s or 60 s, representing shorter or longer time constants for $\dot{V}_{O_2}$ increase.

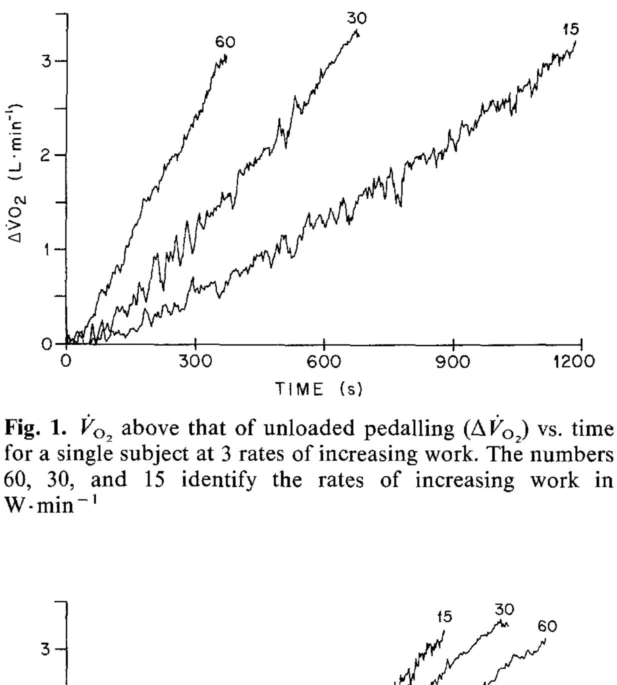

Fig. 1. $\dot{V}_{O_2}$ above that of unloaded pedalling ($\Delta\dot{V}_{O_2}$) vs. time for a single subject at 3 rates of increasing work. The numbers 60, 30, and 15 identify the rates of increasing work in $W \cdot min^{-1}$

Computer analysis

The slopes of the $\Delta\dot{V}_{O_2}/\Delta$wr, analyzed by least squares, are presented in Table 2. Individually and as a group, the slopes were steepest during the 15 $W \cdot min^{-1}$ rate, intermediate during the 30 $W \cdot min^{-1}$ rate, and shallowest during the 60 $W \cdot min^{-1}$ rate.

Because the $\Delta\dot{V}_{O_2}$ vs work rate relationship was not strictly linear at all rates of increase, the lower and upper halves of the curves were analyzed separately as shown in Table 3. Despite the similarity of the slopes at the 15 and 30 $W \cdot min^{-1}$ rates for the lower halves, the slope for the upper half of the 15 $W \cdot min^{-1}$ rate exceeded the 30 $W \cdot min^{-1}$ rate. At both of these rate increments, the slopes for the upper halves were significantly greater than that for the lower halves. The slopes for the upper and lower halves of the 60 $W \cdot min^{-1}$ rate were not significantly different but they were both lower than the 15 and 30 $W \cdot min^{-1}$ incremental tests. To assess the possibility that our findings were dependent on exactly which portions of the relationship we excluded,

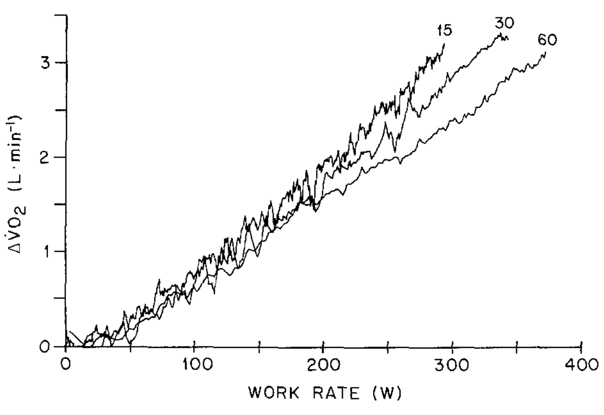

Fig. 2. $\dot{V}_{O_2}$ above that of unloaded pedalling ($\Delta\dot{V}_{O_2}$) vs. work rate at 3 rates of increasing work. Data are from the same tests as Fig. 1. Note that when the work rate increases at 60 $W \cdot min^{-1}$, the maximum $\dot{V}_{O_2}$ is reached at the highest absolute work rate

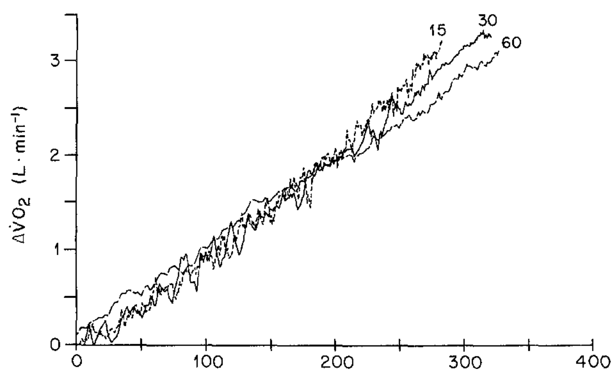

Fig. 3. $\dot{V}_{O_2}$ above that of unloaded pedalling ($\Delta\dot{V}_{O_2}$) vs. work rate at the 3 rates of increasing work. Data are shifted along the abscissa by a work rate equal to 45 s times the rate of increasing work (see text). Data are from the same tests as Figs. 1 and 2. Note that the shifted plots are virtually coincident at lower work rates but have definably different slopes at the higher work rates. The $\Delta\dot{V}_{O_2}$ rises most steeply with the 15 $W \cdot min^{-1}$ test. These same visual relations are seen in the data from all 10 subjects

Table 2. Average slope of O_2 uptake vs work rate relationship ($ml \cdot min^{-1} \cdot W^{-1}$; divide by 60 to obtain $ml \cdot J^{-1}$) during cycle ergometer incremental work rate tests. Work rates were increased in ramp pattern at the rates shown

Subject no.	15 $W \cdot min^{-1}$	30 $W \cdot min^{-1}$	60 $W \cdot min^{-1}$
1	10.6	9.2	8.0
2	10.7	10.2	8.7
3	10.5	10.2	9.2
4	11.8	9.9	8.4
5	11.6	10.5	9.0
6	11.6	10.5	9.6
7	11.0	9.5	8.3
8	11.2	10.9	9.2
9	11.6	10.4	8.6
10	11.0	10.2	8.6
Mean ± SE	11.2 ± 0.15	10.2 ± 0.16	8.8 ± 0.15

Data included in regression analysis are between 100 s after beginning of work rate incrementation and 15 s before the end of test (see text). Each value is mean of 2 tests except for subjects 6 and 7 for the 15 $W \cdot min^{-1}$ ramp. Each mean value is significantly different by analysis of variance and Tukey test ($p < 0.05$)

Table 3. Lower and upper half slopes of O_2 uptake vs. work relationship during cycle ergometer incremental work rate tests. Work rates were increased in ramp pattern at the rates shown

Subject no.	15 $W \cdot min^{-1}$	30 $W \cdot min^{-1}$	60 $W \cdot min^{-1}$
Lower half			
1	9.7	9.8	7.8
2	9.6	10.4	7.5
3	10.1	10.4	9.8
4	11.4	9.9	8.8
5	10.0	9.7	7.4
6	9.4	9.3	8.2
7	9.8	9.2	9.2
8	10.0	10.4	8.9
9	8.9	9.2	8.6
10	9.6	10.2	7.7
Mean ± SE	9.9 ± 0.21	9.9 ± 0.15	8.4 ± 0.25*
Upper half			
1	10.8	8.6	7.4
2	11.2	10.8	8.4
3	11.5	11.2	9.3
4	11.6	9.4	7.9
5	13.4	11.1	9.6
6	13.1	11.1	9.6
7	12.1	9.6	8.0
8	13.0	11.5	8.9
9	14.1	11.4	8.2
10	13.6	10.2	8.8
Mean ± SE	12.45 ± 0.36*	10.49 ± 0.31*	8.7 ± 0.23*

Each value is mean of 2 tests except for subjects 6 and 7 for the 15 $W \cdot min^{-1}$ ramp

* Values are significantly different by analysis of variance and Tukey test ($p < 0.05$). Lower and upper half values are significantly different by paired t test at 15 and 30 $W \cdot min^{-1}$ ($p < 0.05$)

we repeated the computer analyses after 1) excluding the first 135 s (rather than 100 s) and 2) excluding the last 60 s (rather than 15 s). These alternate procedures did not appreciably alter the calculated slopes nor the statistical results.

Discussion

We undertook this analysis to ascertain whether the apparent constancy of the slope of the $\dot{V}_{O_2}$-work rate relationship found by others during cycle ergometry was fortuitous or an invariantly observed phenomenon. For mild and moderate exercise, the constancy of the O_2 cost of external work at 10.0 to 10.5 $ml \cdot min^{-1} \cdot W^{-1}$ seems well-established considering the reports of many investigators who used constant work rate protocols (Asmussen 1965; Astrand and Rodahl 1970; Nagle et al. 1971; Cotes 1975; Gaesser and Brooks 1975; Wasserman and Whipp 1975; Whipp et al. 1981) or slow or rapidly incremented exercise tests (Nagle et al. 1971; Wasserman and Whipp 1975; Spiro 1977; Jones and Campbell 1982; Davis et al. 1982). However, our study did *not* confirm the previously reported (Cotes 1975; Spiro 1977; Whipp et al. 1981; Davis et al. 1982; Jones and Campbell 1982; Younes 1984) linear and quantitatively similar relationship during heavy or exhaustive work.

A major factor which we would expect to *decrease* measured $\dot{V}_{O_2}$ disproportionately during heavy work is the temporary O_2 sparing effect of the energy made available by anaerobic glycolytic mechanisms, i.e. the production of ATP accompanying the conversion of pyruvate to lactate (DiPrampero 1981). DiPrampero suggested that lactate accumulation in young non-athletic subjects should spare a total of 50 ml of O_2 per kg of body weight, equivalent to a volume of approximately 3-5 l of O_2 (O_2 deficit) in our subjects. In exhausting exercise of the durations used, the quantity of lactate accumulated and O_2 deficits should be approximately equal in all tests of a given subject (Astrand and Rodahl 1970; Astrand et al. 1963; Karlsson et al. 1972). Considering the brief durations of the 60 $W \cdot min^{-1}$ tests (Table 1), these 3-5 l of O_2 would be temporarily "spared" during 2 to 3 min; whereas in 15 $W \cdot min^{-1}$ tests, this effect would be spread over approximately 8 to 10 min.

Several factors might be expected to *increase* $\dot{V}_{O_2}$ disproportionately during exhaustive work: concurrent metabolism of lactate to glucose; elevated body temperature and catecholamines; and disproportionate increases in ventilation and myocardial work. These will be briefly considered.

To the extent that lactate is metabolized to glucose or glycogen during exercise, there is an obligatory increase in O_2 requirement without the accomplishment of external work (Krebs 1964; Katz 1986). This may be a dominant factor in the O_2 cost of anaerobic work (Casaburi et al. 1987). The increase in body temperature in exercise of 5 to 20 min duration is likely to be less than 1.5° C (Saltin and Hermansen 1966). Although catecholamine levels rise markedly during heavy exercise (Hartley et al. 1972), their quantitative effects on O_2 consumption during exercise, considering measurements made during rest (Sjostram et al. 1983), are likely to be small. Quantitative estimates of the energy cost of ventilation vary widely (Shephard 1966; Whipp and Pardy 1986), but all show an increase in energy cost per l of ventilation at higher minute ventilations. Shephard estimates that ventilatory energy costs increase from 1—3% at rest to 15% of the body's total energy requirements at a ventilation of 100 $l \cdot min^{-1}$. Extrapolating from the findings of Kitamura et al. (1972) and Nelson et al. (1974), who directly measured myocardial $\dot{V}_{O_2}$, heart rate, and blood pressure during several levels of mild to moderately heavy exercise in healthy young men, we estimate that myocardial $\dot{V}_{O_2}$ increases from approximately 2.5% of the total $\dot{V}_{O_2}$ at low levels of exercise to 3.5% to 4.0% of total $\dot{V}_{O_2}$ at very heavy levels of exercise. In our studies, the maximum heart rates and maximum ventilations for each person differed by less than 10% for each of the work rate increments. Despite the uncertainties of the above estimates, the proportion of total energy expenditure attributable to all of these physiological factors would tend to be similar for each person for his six tests.

The low slopes of the early portion of the 60 $W \cdot min^{-1}$ tests may be partially due to the limited amount of data available for analysis (average of 69 s after excluding the first 100 s of each test). In contrast, the early portions of the 15 $W \cdot min^{-1}$ and 30 $W \cdot min^{-1}$ tests have slopes of 9.9 $ml \cdot min^{-1} \cdot W^{-1}$, values similar to those previously reported for incremental tests of "steady state" tests (Nagle et al. 1971; Whipp et al. 1981; Davis et al. 1982; Hughson and Inman 1986). The upper portions of the 30 $W \cdot min^{-1}$ tests have had $\Delta\dot{V}_{O_2}/\Delta wr$ slopes averaging 10.5 $ml \cdot min^{-1} \cdot W^{-1}$, also consistent with prior reports obtained in young men at this increment rate (Whipp et al. 1981; Davis et al. 1982). However, for the 15 $W \cdot min^{-1}$ tests the upper portions of the $\Delta\dot{V}_{O_2}/\Delta wr$ were significantly higher at heavier work rates; for the 60 $W \cdot min^{-1}$ tests they were significantly lower. Previous investigators may not have discerned these differences because they utilized a narrower range of work rate increments or because data were not analyzed by computerized regression procedures.

We believe our findings may be explained by considering: a) the magnitude and duration of the O_2 deficit accumulation, and b) probable differences in the efficiency of work at low and high work intensities. First, we postulate that the lower $\Delta\dot{V}_{O_2}/\Delta wr$ slope seen in the 60 $W \cdot min^{-1}$ tests results from the major energy contribution of anaerobic glycolysis (several l of oxygen deficit) over a very short period of time, approximately 2 to 3 min. Second, the finding that the $\Delta\dot{V}_{O_2}/\Delta wr$ increases during the latter portions of the 15 $W \cdot min^{-1}$ strongly suggests a higher energy cost per W of heavy or very heavy work than per W of mild of mild or moderate work. During these slower tests, the temporary $\dot{V}_{O_2}$ sparing effect of the accumulating O_2 deficit is, on average, spread over 8 to 10 min and thus influences the $\Delta\dot{V}_{O_2}/\Delta wr$ less than during rapid tests. Third, the near-linearity usually found in the intermediate duration tests (30 $W \cdot min^{-1}$) is not due to an unchanging work efficiency, but can be explained by what appears to be a fortuitous balance between the higher energy cost per W of heavier work and the temporary $\dot{V}_{O_2}$ sparing effect of the accumulating O_2 deficit. Although this explanation must be considered conjectural at this point, recognition of the non-linearity of the $\Delta\dot{V}_{O_2}/\Delta wr$ relationship is a necessary first step towards establishing the mechanisms dictating the $\dot{V}_{O_2}$ during heavy exercise.

Appendix

To emphasize deviations from linearity in the $\dot{V}_{O_2}$ responses, we considered the implications of varying the slope of a ramp-pattern stimulus to a presumed first order linear system. For such a system, the time course of response, above an unloaded pedalling baseline is

$$\dot{V}_{O_2} = \dot{V}_{O_{2ss}} wr_s [t - \tau(1 - e^{-t/\tau})] \quad (1)$$

where t is time after the work rate ramp begins, τ is the time constant of the system, $\dot{V}_{O_{2s}}$ is the slope of the steady-state $\dot{V}_{O_2}$ — work rate relation ($ml \cdot min^{-1} \cdot W^{-1}$) and wr_s is the rate of increase in work rate (work rate slope). If the $\dot{V}_{O_2}$ response is related to work rate (wr) rather than time,

$$\dot{V}_{O_2} = \dot{V}_{O_{2s}}[wr - wr_s \tau (1 - e^{-wr/wr_s \tau})] \quad (2)$$

note that for $t > 2-3\,\tau$, (i.e., $wr/wr_s > 2-3\,\tau$) this reduces to

$$\dot{V}_{O_2} = \dot{V}_{O_{2s}}(wr - wr_s \tau) \quad (3)$$

Thus it can be seen that, except for the initial few minutes of data, the $\dot{V}_{O_2}$-work rate relation for various ramp slopes should be parallel and displaced from each other by ($wr_s \tau'$) watts. The $\dot{V}_{O_2}$-work rate responses are plotted in Fig. 3 on axes where each curve was shifted by an amount ($wr_s \tau$); deviations from linearity are thus more readily distinguished.

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