Def Sci J, Vol 33, No 3, July 1983, pp 205–219

Biomathematical Study of the Kinetics of Energy Output During Physical Exercise

G. P. Dimri & N. C. Majumdar
Defence Institute of Physiology and Allied Sciences, Delhi Cantt-110010.

Received 17 September 1982; revised 17 February 1983

Abstract. The kinetics of energy production during different grades of activity has been described in terms of rate constant and workload for submaximal, maximal and supermaximal exercises. Equations have been derived for the aerobic and anaerobic components of energy production for the three cases. The theoretical approach has been validated with the available experimental data.

1. Introduction

When mechanical work is performed say on a bicycle ergometer at a given rate, the body has to produce energy at a rate determined by the mechanical efficiency for the particular task. The difference between energy produced and mechanical work performed is dissipated as heat[1]. However, when a resting man starts the work, he cannot instantaneously raise his energy production to the level demanded by the workload. A finite time interval is required to attain the peak value of energy production[2,3]. During this interval, part of the energy demand is met aerobically by oxygen consumption[4,5]. The balance is met anaerobically resulting in progressively increasing oxygen deficit which is repaid during recovery period[6-8].

The problem that poses itself is how rate of energy production is related to time during the transient phase before attaining the steady state. The kinetics of energy production has been studied by some workers[9-12]. The findings are contradictory in respect of half time of oxygen uptake (V_{0_2}). Whereas it has been reported by some workers[9,13] that the pattern of V_{0_2} rise in steady state can be described by an exponential function and that the rate constant is the same for all workrates. Others[10-12] have observed an increase in the half time of V_{0_2} response as work intensity increased. The work intensity in these studies mostly appear to be submaximal work. It is thus seen that the kinetics of energy production has not been studied for supermaximal work.

The object of the present study is to investigate the kinetics of energy production and the related aerobic and anaerobic components from the stand point of a bio-mathematician in all grades of work viz. submaximal, maximal and supermaximal.

2. Proposed Theoretical Approach

Let y be the instantaneous value of energy production at time t after starting the exercise. Let y_0 be the initial value (pre-exercise value) of y, and y_w, the value demanded by the specific workload. As soon as work is started, the physiological process involved, attempts to make y approach to y_w as demanded by the exercise. At any instant t the rate of approach to y_w i.e. dy/dt should be proportional to the instantaneous gap between y_w and y. This may be expressed mathematically as

$$\frac{dy}{dt} = k\,(y_w - y) \tag{1}$$

where k is the rate constant likely to depend on the individuals physical status and possibly on the nature of work. Integration of Eqn. (1) yields

$$\ln\,(y_w - y) = \quad kt \tag{2}$$

with initial condition that

$y = y_0$ at $t = 0$, Eqn. (2) reduces to

$$\ln\,(y_w \;\; y_0) = c \tag{3}$$

substituting this value in Eqn. (2), we get

$$\ln\,(y_w - y) = -kt + \ln\,(y_w - y_0)$$

which on simplification yields

$$y = y_w - (y_w - y_0)\exp(-kt \tag{4}$$

Eqn. (4), can therefore be used to predict the rate of energy production y at any instant t after the start of the exercise. Fig. 1 gives the theoretical shape of the exponential growth curve relating y to t. The figure has been drawn with three assumed values of k ($k_1 < k_2 < k_3$). It is seen that higher the value of k, quicker the approach to the equilibrium level, k being the rate constant.

While the above is true for submaximal exercise ($yw < y_m$) and maximal exercise ($y_w = y_m$), this will be far from justified in the case of supermaximal work ($y_w > y_m$), where y_m is the individual's maximum value of energy production. The theoretical growth part of the curve follows the same theoretical equation till the maximal value y_m is reached (Fig. 2). Thereafter, instead of following the theoretical curve shown by the dotted portion, y remains stationary at the value y_m till the endurance is reached, shown by the cut off point C. The actual growth curve is represented by the thick line ABC.

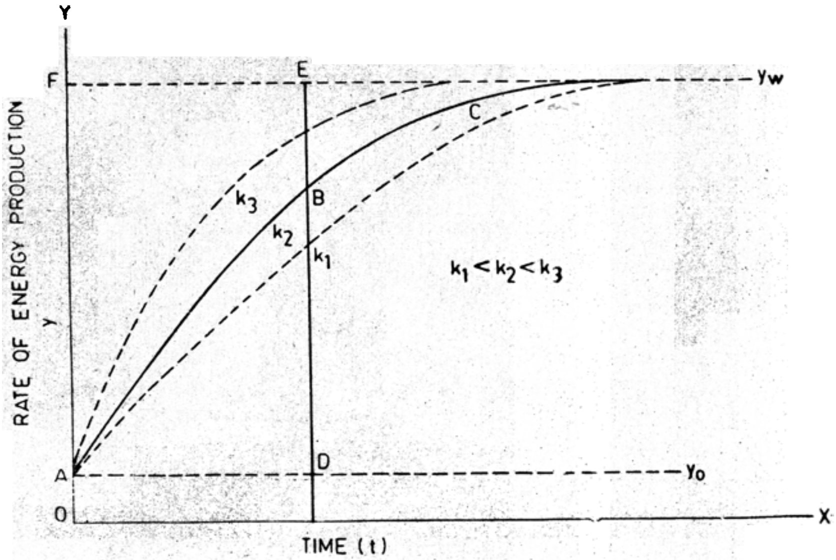

Figure 1. Theoretical relationship between y and t for three values of k (schematic).

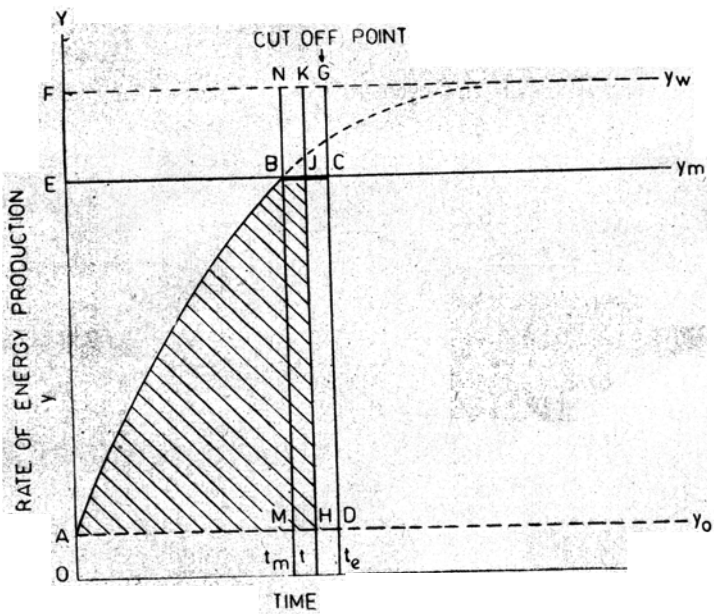

Figure 2. Relationship between y and t in supermaximal exercise for fixed k (schematic).

Time Course of Aerobic and Anaerobic Energy Production

Case I. Submaximal Work : Let us consider the growth curve ABC in Fig. 1, corresponding the velocity constant k_2. The vertical line ED is drawn at the time t, intersecting the curve ABC at B. The aerobic energy cost of the work upto time t will be given by the area enclosed by the curve AB, vertical line BD and horizontal line AD. Denoting it by $E_a(t)$, we have

$$E_a(t) = \int_0^t (y - y_0)\, dt \tag{5}$$

substituting the value of y from (4) in (5) we get

$$E_a(t) = (y_w - y_0) \int_0^t [1 - \exp(-kt)] \tag{6}$$

which after integration and simplification becomes

$$E_a(t) = (yw - y_0) \left[t - \frac{1}{k} \{1 - \exp(-kt)\} \right] \tag{7}$$

Let us now evaluate anaerobic cost of submaximal work upto time t. We note that the total cost of the work upto time t is given by the area of the rectangle ADEF in Fig. 1, being equal to $(y_w - y_0)t$. Hence the anaerobic cost $E_{an}(t)$ will be obtained by substracting $E_a(t)$ from the total cost. In other words

$$E_{an}(t) = (y_w - y_0)\, t - E_a(t)$$

substitution of the value of $E_a(t)$ from Eqn. (7) leads to

$$E_{an}(t) = \frac{(y_w - y_0)}{k} [1 - \exp(-kt)] \tag{8}$$

By making $t \rightarrow \infty$, we obtain the value of maximum anaerobic cost of the given submaximal work load as

$$E_{an}(\infty) = \frac{(y_w - y_0)}{k} \tag{9}$$

Case 2 : Maximal Work : All the equations developed under submaximal work are applicable to maximal work as well, provided y_w is replaced by y_m, the maximum rate of energy production by the individual. In particular, aerobic cost of maximal work upto time t will be given from Eqn. (7) by

$$E_a(t) = (y_m - y_0) \left[t - \frac{1}{k} \left\{ 1 - \exp(-kt) \right\} \right] \tag{10}$$

and the anaerobic cost of the same maximal work upto time t will be given from Eqn. (8) by

$$E_{an}(t) = \frac{(y_m - y_0)}{k} [1 - \exp(-kt)]$$

Further, the maximum anaerobic cost of the maximal work ($t \to \infty$) will be

$$E_{an}(\infty) = \frac{(y_m - y_0)}{k}$$

It may be noted, however that maximal work cannot be performed for an indefinite period, endurance time depending upon the level of physical training of the individual.

Case 3: *Super Maximal Work* ($y_w > y_m$) :

In this case, the growth curve upto the cut off point (endurance time t_e) consists of two distinct intervals, i.e., from A to B and from B to C in Fig. 2. Let the values of t corresponding to points B and C be denoted by t_m and t_e respectively. Here t_m represents the time taken to reach the maximal rate of energy production y_m and t_e denotes the endurance time corresponding to the cut off point.

By substituting t_m for t and y_m for y in Eq (4), we get

$$y_m = y_w - (y_w - y_0) \exp(-kt_m)$$

whence

$$\frac{1}{k} \ln \frac{(y_w - y_0)}{(y_w - y_m)}$$

Let us now consider the two intervals $0 < t \leqslant t_m$ and $t_m < t < t_e$ separately.

Interval $0 < t \leqslant t_m$: In this case all the equations of submaximal (*Case I*) will be applicable.

Interval $t_m < t < t_e$: The situation is schematically described in Fig. 2, in which vertical lines HJK and MBN correspond to t and t_m respectively. The aerobic cost, $E_a(t)$ of the work upto time t will be given by the shaded area ABJHA which is the sum of two areas ABM, as given by Eqn. (7) with t replaced by t_m, and area MBJH equal to $(y_m - y_0)(t - t_m)$. Hence the aerobic cost of the work will be given by

$$E_a(t) = (y_w \quad y_0)\left[\qquad \frac{}{k}\left\{ -\exp(\ \cdot k\ t_m) \right\}\right] \quad (y_m - y_0)(t - t_m)$$

which on simplification leads to

$$E_a(t) = (y_m - y_0)\,t + (y_w - y_m)\,t_m \quad \cdot\frac{(y_w - y_0)}{k}[1 - \exp(-kt_m)] \tag{14}$$

In the same way the anaerobic cost $E_{an}(t)$ of the work upto time t will be given by the area ABJKF which is the sum of the two areas, ABNF and BJKN. The former is given by the Eqn. (8) while the latter being that of a rectangle, is equal to $(y_w - y_m)(t - t_m)$. Thus the anaerobic cost will be given by

$$E_{an}(t) = \frac{(y_w - y_0)}{k}[1 - \exp(-kt_m)] \quad (y_w - y_m)(t\cdot \quad t_m) \tag{15}$$

3. Evaluation of the Parameters of the Kinetics of Energy Production

One of the most important parameters in the kinetics of energy production during the transient phase is the rate constant k. Its knowledge is essential in the study of the build up of energy production, both aerobic and anaerobic. It is particularly useful in working out the aerobic and anaerobic fractions of total energy cost of the physical work at all levels, viz., submaximal, maximal and supermaximal. Two other parameters in the case of submaximal work are y_0, the pre-exercise energy production and y_w, the energy demand of the workload. For maximal and supermaximal work, a third parameter is y_m, the individual's maximum rate of energy production. Methods for their evaluation are suggested below :

Method 1. General Method: This method will be particularly useful when the workload is not known or specified. We choose three equispaced points on the growth curve, viz.

(t_1, y_1), (t_2, y_2) and $t_3, y_3)$ such that $(t_2-t_1) = (t_3-t_2)$. From Eqn. (4) it follows that

$$y_1 = y_w - (y_w - y_0) \exp(-kt_1)$$
$$y_2 = y_w - (y_w - y_0) \exp(-kt_2)$$
$$y_3 = y_w - (y_w - y_0) \exp(-kt_3)$$

The above may be rearranged as

$$\frac{(y_w-y_0)}{(y_w-y_1)} = \exp(kt_1)$$

$$\frac{(y_w-y_0)}{(y_w-y_2)} = \exp(kt_2)$$

$$\frac{(y_w-y_0)}{(y_w-y_3)} = \exp(kt_3) \tag{19}$$

Dividing (18) by (17) and also (19) by (18), we obtain

$$\frac{(y_w-y_1)}{(y_w-y_2)} = \exp[k(t_2-t_1)]$$

and

$$\frac{(y_w-y_2)}{(y_w-y_3)} = \exp[k(t_3-t_2)]$$

since the RHS of both the above equations are equal, it follows that

$$\frac{(y_w-y_1)}{(y_w-y_2)} = \frac{(y_w-y_2)}{(y_w-y_3)}$$

from which y_w is solved as

$$y_w = \frac{y_1 y_3 - y_2^2}{y_1 + y_3 - 2y_2} \tag{23}$$

From Eqn (20), we find the expression for k as

$$k = \frac{1}{(t_2 - t_1)} \ln \frac{(y_w - y_1)}{(y_w - y_2)}$$

After eliminating y_w with the help of Eqn. (23), we obtain the final expression for k as

$$k = \frac{1}{(t_2 - t_1)} \ln \frac{(y_2 - y_1)}{(y_3 - y_2)} \tag{24}$$

From the first E_q of (16) after substituting value of y_w and k from Eqns. (23) and (24) we have the expression for y_0 as

$$y_0 = y_w - (y_w - y_1) \exp(kt_1) \tag{25}$$

We see from the foregoings that with the help of any three equispaced points on the (y, t) graph, all the three parameters, viz., y_w, k and y_0 can be estimated as given by Eqns. (23), (24) and (25). Since a ratio of small differences is involved, reasonable accuracy can be achieved only by making the time interval $(t_2 - t_1)$ relatively large. Hence the method is not suitable for supermaximal exercise for which the total duration of work is small.

Method 2 : For Specified Workload: Let the specified workload be y_w in terms of rate of energy production. Equation (4) can be put in the form

$$\ln(y_w - y) = \ln(y_w - y_0) \tag{26}$$

so that $\ln(y_w - y)$ plotted against t should yield a straight line with a negative slope equal to $-k$. The intercept on the ordinate axis ($t = 0$) gives the value of $\ln(y_w - y_0)$. Hence y_0 can be estimated. Since Eqn. (26) is a first degree linear equation the two constants can be determined more accurately by the statistical method of least squares.

Method 3. For Known Workload and Pre-exercise Energy Production: Let y_w be the rate of energy production for specified workload and y_0, the pre-exercise rate of energy production, then Eqn. (4) can be put in the form

$$\ln \frac{(y_w - y_0)}{(y_w - y)} = kt \tag{27}$$

Thus $\ln \frac{(y_w - y_0)}{(y_w - y)}$ plotted against t should yield a straight line passing through the origin. The slope of the line gives k. However the best value of k will be obtained statistically with the help of the formula

$$k = \frac{\Sigma \ln [(y_w - y_0)/(y_w - y)]}{\Sigma t} \tag{28}$$

For reliable estimate of k, values of y too close to y_w should be omitted because otherwise the error will be magnified many times. However this problem will not arise in the case of supermaximal work.

4. Validation of the Proposed Theory

In order to validate the proposed theoretical approach outlined in the foregoing, available experimental data for submaximal and supermaximal exercise on bicycle ergometer were utilised. The data for submaximal exercise were obtained in our laboratory while those for submaximal and supermaximal exercise were obtained from Astrand and Rodhal[14].

Submaximal Exercise

Minute by minute data on oxygen uptake in $l.\ \text{min}^{-1}$ at a fixed level of work of 800 kgm min^{-1} on bicycle ergometer were obtained for 6 normal, healthy young male subjects with mean age, height and weight being 24.2 yr, 166.2 cm, 52.7 kg respectively. The average values alongwith standard error of mean are presented in Table 1.

Table 1. Time course of oxygen uptake ($l\ \text{min}^{-1}$) during submaximal exercise of 800 kgm min^{-1}. Values are averages of six subjects.

S. No.	Time (min)	Observed oxygen uptake ($l\ \text{min}^{-1}$)	Estimated oxygen uptake ($l\ \text{min}^{-1}$)	Maximum oxygen uptake capacity (V_{o_2} max) ($l\ \text{min}^{-1}$)
	0.5	0.909 $\pm$0.108	0.877	
2.	.5	1.371 $\pm$0.085		
3.	2.5	1.741 $\pm$0.092	.735	
4.	3.5	1.861 $\pm$0.093	1.889	2.448 $\pm$0.090
5.	4.5	2.063 $\pm$0.116		
6.	5.5	2.003 $\pm$0.108	2.011	
7.	6.5	2.005 $\pm$0.082		
8.	7.5	1.963 $\pm$0.121		
9.	8.5	2.070 $\pm$0.108	2.050	
	9.5	2.064 $\pm$0.139	2.054	

Mean $y_w = 2.042$

(The mean y_w has been calculated as the mean of individual values of observed oxygen uptake of 6 subjects from 5 min to 10 min).

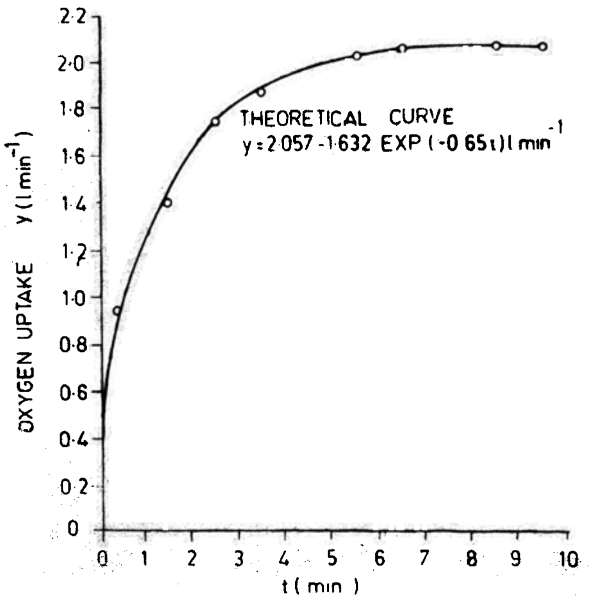

Figure 3. Theoretical curve and experimental points in submaximal exercise (800 kg m min^{-1} on bicycle ergometer (average of six subjects).

Expressing energy production in terms of oxygen uptake in $l\ \text{min}^{-1}$, the observed values have been plotted against time t in Fig. 3, which clearly exhibits an exponential trend. A smooth curve was fitted to these points with the help of french curves. From this curve, 4 sets of three equispaced points each, were read and recorded in Table 2. The value of k was estimated from each set according to general method 1.

Table 2. Estimation of rate constant k from observed (t, y) values.

S. No.	Time t (min)	Oxygen uptake y ($l\ \text{min}^{-1}$)	Rate constant ($k\ \text{min}^{-1}$)
	0	0.287	
	2	1.57	
	4	1.91	
	0.5	0.909	
2	2.5	1.74	
	4.5	1.95	
	0.5	0.909	
3	3.0	1.80	
	5.5	2.0	
	1.0	1.14	
4	3.0	1.80	
	5.0	1.98	

Weighted mean k = 0.650

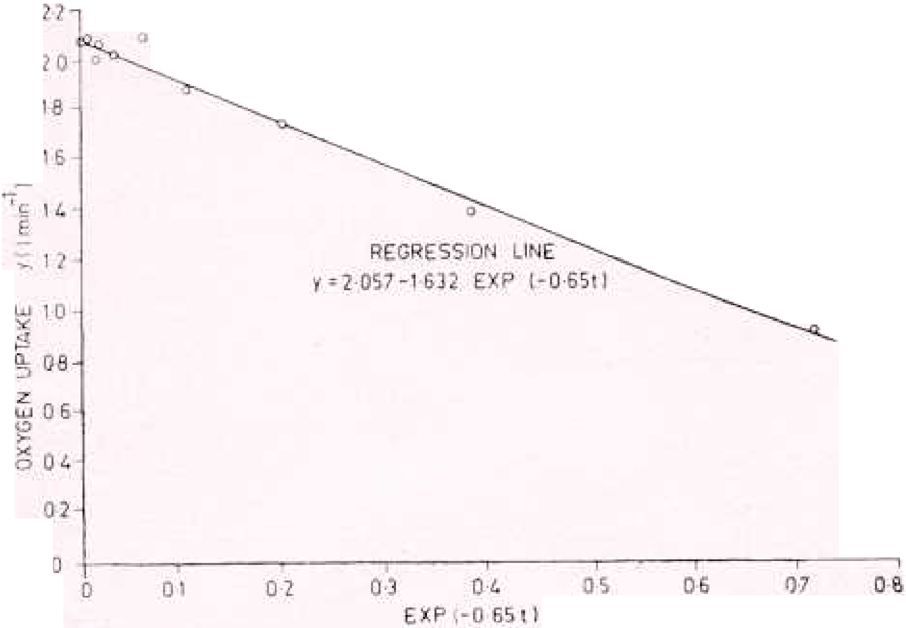

Figure 4. Linearity between y and exp $(-0.65t)$

The values obtained are reasonably close to one another, the average of the four values being 0.650 min^{-1}. With the knowledge of k, we now proceed to evaluate the constants of Eqn. (4), viz., $y = y_w - (y_w - y_0)\exp(-kt)$. Exp $(-0.650\ t)$ was computed for all the points in Table 1 and corresponding y values were plotted in Fig. 4, which exhibits an apparently good linear relationship. A straight line was fitted to these points by least square method. The final equation obtained is

$$y = 2.057 - 1.632 \exp(-0.650\ t)\ l\ \text{min}^{-1} \tag{29}$$

This equation is shown by the regression line (Fig. 3) and is represented by exponential curve with $y_w = 2.057$. The goodness of fit is quite apparent. The values of y, estimated from Eqn (29). have also been presented in Table 1. The correlation coefficient between observed and estimated values of oxygen uptake is 0.99 which is highly significant ($P \angle 0.001$).

Supermaximal Exercise

Astrand and Rodahl[14] have given experimental curves showing increase in oxygen uptake of a single subject during heavy exercise on bicycle ergometer following a 10 min warm up period. Oxygen uptake in l min^{-1} has been plotted against time in minute for 5 different workloads. V_{O_2} max of the subject was 4.10 l min^{-1}. Experimental data extracted from the figure have been presented in Table 3. Initial values of oxygen uptake was about 2.2 l min^{-1} in all the five grades of work. Mechanical workload has been expressed in kpm min^{-1} and ranged from 1650 to 2700 kpm min^{-1}. However, since y_w represents the energy requirement of the exercise, we have made use of the conversion table given by Astrand and Rodahl[14]. The same has been

Table 3. Experimental data on a single subject (y_m = 4.1 l min^{-1} and y_0 = 2.20 l min^{-1}. (Data from Astrand and Rodahl).

S. No.	Workload (kpm mn^{-1})	y_w (l min^{-1})	t (min)	y (l min^{-1}) (obs)	y (l min^{-1}) (est)	Endurance time t_e (min)	Time to reach V_{o_2} max t_m (min) (est)
1.	2700	6.53	0.25	2.75	2.76	1.76	1.04
			0.80	3.93	3.76		
			1.30	4.10	4.43		
		5.73	0.75	3.52	3.40	2.30	1.39
			1.20	3.82	3.92		
			1.65	4.10	4.32		
	2100	4.96	0.25	2.50	2.54	3.00	2.10
			0.75	3.44	3.14		
			1.25	3.75	3.58		
			1.75	3.95	3.92		
			2.75	4.10	4.36		
		4.21	1.50	3.37	3.34	6.00	5.23
			2.50	3.63	3.71		
			3.33	3.85	3.89		
			4.27	3.93	4.02		
			4.75	4.00	4.07		
			5.25	4.10	4.10		
5.	1650	3.85	0.50	2.65	2.60	8.00	(Submaximal)
			1.50	3.18	3.13		
			2.50	3.34	3.44		
			3.50	3.59	3.61		
			4.50	3.62	3.71		
			6.50	3.75	3.81		
			7.50	3.80	3.82		

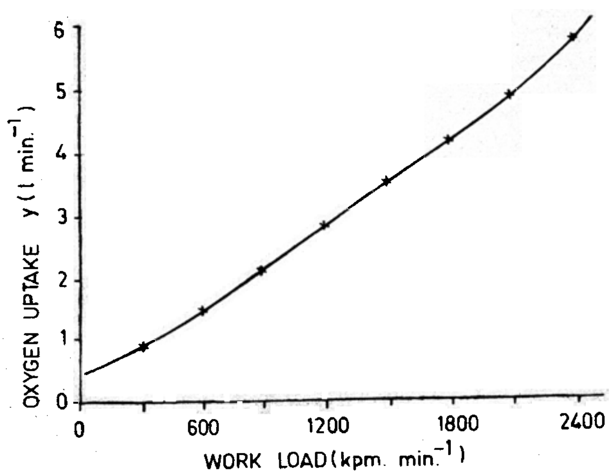

Figure 5. Relationship between oxygen uptake and workload for bicycle ergo· meter. (Data from Astrand and Rodahl 1970)

shown in Fig. 5, in which required oxygen uptake in $l\,\mathrm{min}^{-1}$ has been plotted against workload in kpm min^{-1}. The relationship is practically linear although a slight curvature is perceptible. We have therefore fitted a second degree equation to the points by the least square method and the resulting equation is

$$y_w = 1.52 \times 10^{-7}\, W^2 + 1.895 \times 10^{-3}\, W + 0.305\ l\ \mathrm{min}^{-1} \tag{30}$$

where W is the mechanical workload in kpm min^{-1}. The regression line is also shown in Fig. 5 indicating a nearly perfect fit. The values of y_w corresponding to the five experimental workloads as derived from Eqn. (30) have also been shown in Table 3 alongwith endurance time.

To estimate the value of k, the values of y should not be too close to y_w, for otherwise the error is magnified as will be clear from an inspection of Eqn. (28). There is no problem in the case of supermaximal work. In the case of submaximal or near maximal work, we note that most of the growth of oxygen uptake curve is accomplished within 4 min from the start of the exercise. As such for estimation of k, we have used the values of y, i.e., oxygen uptake for $t < 4$ min. Further we have used all values of $y < y_m$, i.e., V_{O_2} max. The values of k obtained by this method for each workload are given in Table 4.

Table 4. Estimation of rate constant k from observed (t, y) values for different workloads.

S. No.	Workload (kpm. min^{-1})	Rate constant k (min^{-1})
1.	2700	0.615
2.	2400	0.555
3.	2100	0.635
4.	1800	0.531
5	1650	0.530

It may be noted that k is reasonably independent of the workload. As such we have pooled all the data and estimated k with the help of Eqn. (28). The values of k thus obtained is 0.556 min^{-1}. The equation relating y to t becomes

$$y = y_w - (y_w - 2.2) \exp(-0.556)\ l\ \mathrm{min}^{-1} \tag{31}$$

The curve representing Eqn. (31) has been shown in Fig. 6 alongwith the experimental points. The fit is reasonably good indicating thereby that the proposed theoretical approach is justified. The estimated values of y from Eqn. (31) have been compared to observed values of y in Table 3. The correlation coefficient between the observed and estimated values of y works out to be 0. 99 which is highly significant ($P < 0.001$).

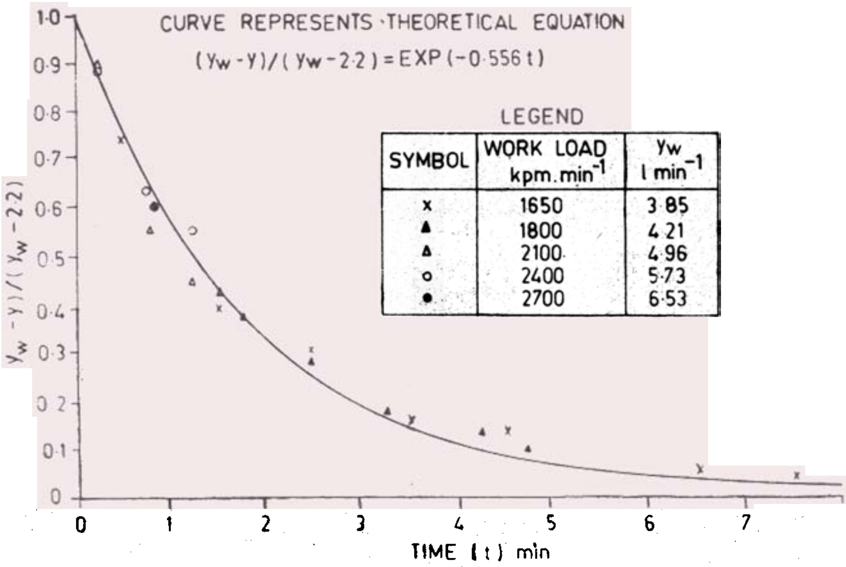

Figure 6. Theoretical curve and experimental points for a single subject at five different workloads. (Data from Astrand and Rodahl 1970).

5. Discussion

The principal aim of the present study has been to lay down the biomathematical basis for understanding the kinetics of oxygen uptake during exercise of all grades from submaximal to supermaximal. The mathematical description of the rate of energy production during exercise as given by Eqn. (4), is based on the assumption of the stochastic independence and identicalness of the underlying increments of the energy production and homogenity with respect to time structure in which the system operates (Gold[15]). Equations have been derived relating to the rate of energy production and its aerobic and anaerobic components with time after the onset of exercise, in different grades of exercise Validation of all the equations has not been possible due to paucity of data. However the general theory is substantially validated with the available data on submaximal and supermaximal exercise. In Fig. 3 for a fixed grade of submaximal exercise on bicycle ergometer, average of experimental data of O_2 uptake on six Indian male subjects have been plotted alongwith the theoretical curve with rate constant k equal to 0.650 min^{-1}. In Fig. 6 data on a single subject for five different workloads have been plotted alongwith the theoretical curve with k equal to 0.556 min^{-1}.

Both the figures appear to justify the proposed theoretical approach. From an inspection of the values of k for supermaximal workloads, it is found that the rate constant is independent of the intensity of work and thus agrees with Margaria *et.al,*[9] Diprampero *et al*[13]. This is however in contrast with Whipp *et al*[10] and Hagberg *et al*[11]. The reason for disagreement is possibly the duration of exercises, in which the steady state V_{O_2} is not reached at supermaximal workloads. We have therefore replaced steady state oxygen uptake by energy requirement of the workload i.e. y_w as calculated from Astrand *et al*[14]. The close agreement between observed and estimated values of oxygen uptake validates this contention.

The higher value of k corresponds to the subject group having lower value of V_{O_2} max (2.45 l min^{-1}) while the lower value of k corresponds to a higher value of V_{O_2} max (4.10 l min^{-1}). This may be due to differences in ethenic origin. Increase in physical fitness level means an improved oxygen carrying capacity by the human system. Improved oxygen carrying capacity of the system entails a higher rate constant from Fig. 1 which implies lower oxygen debt. The dynamics of Eqn. (13) reveals that increase in physical fitness level would mean greater y_m which will improve endurance time t_m.

In the case of supermaximal exercise, Eqn. (13) enables us to predict t_m, the time to reach V_{O_2} max. The computed values of t_m have also been presented in Table 3. It will be seen that the values of t_m are quite close to the values of endurance time, differences lying between 0.7 to 0.9 minutes. This suggests a practical application of k for predicting endurance capacity.

It can thus be concluded from the available data that the rate constant in the kinetics of oxygen uptake (energy expenditure) is independent of work intensity at supermaximal workloads and is likely to depend on the physical fitness of the subject.

Acknowledgements

The authors are grateful to Gp. Capt. K. C. Sinha, Director, DIPAS, Delhi Cantt for his encouragement and permission to publish the paper. Thanks are also due to Miss Anita Madan for secretarial services.

References

1. Hill, A. V., *Proc. Roy. Soc.* (Biol), **148** (1958) 397.
2. Henry, F. M. & DeMoor, J. C., *Appl, Physiol.*, **8** (1956), 608-614.
3. Wasserman, K., VanKassel, A. L. & Burton, G. C., *J. Appl. Physiol.*, **22** (1967), 71-85.
4. Astrand, I,, *Acta. Physiol. Scand.*, **49** (1960), Suppl. 169.
5. Saltin, B., *Acta. Physiol. Scand.*, (1964), Suppl. 230.
6. Margaria, R., Edwards, H. T., & Dill, D. B., *Am. J. Physiol.*, 106 (1933), 689-715.
7. Welch, H. G., Faulkner, J. A., Barclay, J. K., & Brooks, J. A., *Med. Sci. Sports*, **2** (1970), 15-19.
8. Whipp, B. J. & Wasserman, K, *J. Appl. Physiol.*, **28** (1970), 452-456.
9. Margaria, R., Mangili, F., Cuttica, F. & Cerretelli, P., *Ergomomics*, **8** (1965), 49-54.
10. Whipp, B. J. & Wasserman, K., *J. Appl. Physiol.*, **33** (1972), 351-356.

11. Hagberg, J. M., Nagle, F. J. & Carlson, J. L., *J. Appl. Physiol, and Respirate Environ. Exec. Physiol.*, **44** (1978), 90-92.
12. Fox, E. L., Kirkendall, D. T. & Bartels, R. L., *Eur. J. Appl. Physiol.*, **44** (1980), 77-81.
13. Diprampero, P., Davies, C. T. M., Cerretelli, P., & Margaria, R., *J. Appl. Physiol.*, **29** (1970), 547-551.
14. Astrand, P. O. & Rodahl, K., 'Textbook of Work Physiology' (McGraw Hill KogaKusha Ltd., New York), 1970.
15. Gold, H. J., 'Mathematical modelling of biological systems—An introductory guidebook' (John Wiley & Sons), 1977.