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Lactic Acid Production in Supramaximal Exercise*

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Summary. On 12 subjects of different muscular fitness the rate of lactic acid appearance in blood, while performing the same supramaximal exercise has been determined, together with the maximal performance time and the maximal L.A. concentration in blood. The rate of increase of lactic acid is higher in the less fit than in the athletic subjects, to compensate for the lower oxygen consumption. In all subjects the appearance of L.A. in the blood is delayed: at the onset of the exercise other anaerobic processes (alactic) supply the energy required, and only when these are exhausted L.A. formation enters into play. The energy due to lactic acid corresponds to 37 $\pm$ 3.5 ml of O_2 per g of lactic acid increase in 1 l of blood, or 50 ml of O_2 (or 250 cal) per g of L.A. produced from glycogen. The maximal amount of the lactacid debt is equivalent to about the maximum oxygen consumption in 1 min. A simple relation is found between the time of performance in supramaximal exercise and the maximum oxygen consumption.

Key-Words: Exercise, Supramaximal — Lactic Acid, Rate of Production — Lactic Acid, Energy Equivalent of O_2 Debt — Muscular Exercise, Energy Sources in.

It has been found that the L.A. appearance in blood in supramaximal exercise (i.e. greater than that corresponding to the maximal O_2 consumption, $\dot{V}_{O_2}^{max}$) is linearly related with the time of performance t, according to the eq.

$$g_{\text{L.A.}}/\text{l} = a + bt \qquad (1)$$

where $g_{\text{L.A.}}/\text{l}$ is the concentration of L.A. in g per l of blood [7,8]. Furthermore the rate of L.A. appearance in blood $b = dg_{\text{L.A.}}/dt$ increases also linearly with the increase of energy requirement. This has been interpreted as evidence that in supramaximal exercise L.A. production alone is responsible for providing the energy required in excess of that obtainable from oxidations.

Energy sources in muscular activity other than L.A. formation are 1. phosphagen (ATP + CP) break-down, and 2. oxidations: in supramaximal exercise the phosphagen content of the muscles reaches in

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a few seconds a steady condition in which the rate of phosphagen resynthesis equals the rate of splitting; after this condition is reached, no net energy production can be attributed to this mechanism: as regards 2. the O_2 consumption has reached its maximal value, which does not increase with further increasing work load. Then, neglecting the first few seconds of supramaximal exercise, the total energy requirement $\dot{W}$ expressed in O_2 equivalents may be described by the equation:

$$\dot{W} = \dot{V}_{O_2}^{max} + m\,(g_{L.A.}/l) \tag{2}$$

where $\dot{V}_{O_2}^{max}$ is a constant for a given subject and $\underline{m}$ is the O_2 equivalent of 1 g L.A. increase in 1 l of blood.

If this interpretation is correct, by keeping constant the work load, i.e. the energy requirement, the rate of lactic acid formation should change linearly with the maximal oxygen consumption when the experiments are carried on a group of subjects of sensibly different values of $\dot{V}_{O_2}^{max}$. The present work has been planned in order to describe the quantitative relation between the rate of lactic acid appearance in blood and the maximal oxygen consumption in different subjects performing the same supramaximal exercise.

Methods

The experiments have been performed on 12 male subjects 21—33 years old: 4 were athletes in good training condition, 4 were fairly active in sports, and 4 had no sport activity at all.

A test for aerobic and anaerobic power ($\dot{V}_{O_2}^{max}$ and $\dot{W}_{P}^{max}$) [5,6] was given previously to all subjects. The maximal aerobic power, expressed in O_2 consumption, ml/kg · min, ran from a minimum of 26.6 to a maximum of 66. The maximal anaerobic power, calculated as energy requirement and also expressed in ml of O_2/kg · min, ran from a minimum of 128 to a maximum of 221.

The subjects came to the Lab. in the morning after a light breakfast. The exercise consisted in running on a treadmill at 16 km/h at an incline of 10%, an exercise familiar to all subjects, involving a net energy requirement of 80 ml/kg · min of O_2, and therefore greater than the $\dot{V}_{O_2}^{max}$ for all subjects.

The effect of time of performance on blood lactic acid was studied by stopping the exercise at suitable intervals. After a 4 min rest, to allow for a uniform distribution of lactic acid in the body fluids [8], blood was drawn for the determination of L.A. according to Gercken's enzymatic method [2].

Four experiments to exhaustion have been carried out for each subject, and the maximal performance time and L.A. concentration in the blood measured.

Results

As found earlier by Margaria *et al.* [7,8] the lactic acid concentration in the blood ($g_{L.A.}/l$) in supramaximal work increases linearly with the time of performace (t) as indicated in formula (1).

Table. *For every subject the maximal aerobic power, the values of the constants* a *and* b *of equation (1), the maximal time of performance and the blood lactic acid at exhaustion are given together with the standard deviation*

	Subjects	$\dot{V}_{O_2}^{max}$ ml/kg · min	*a* $g_{L.A.}$/l	*b* $g_{L.A.}$/l · min	Exhaustion *t* (min)	Exhaustion L.A. (g/l)
Athletes	S.M.	66	− 0.098 (± 0.031)	0.497 (± 0.018)	2.124 (± 0.259)	1.019 (± 0.162)
	F.C.	63.3	− 0.179 (± 0.056)	0.539 (± 0.026)	2.334 (± 0.105)	1.071 (± 0.085)
	R.G.	60	+ 0.042 (± 0.051)	0.565 (± 0.026)	2.268 (± 0.312)	1.354 (± 0.125)
	P.P.	56.5	− 0.133 (± 0.070)	0.731 (± 0.060)	1.512 (± 0.126)	1.033 (± 0.127)
Sportmen	F.G.	54	− 0.024 (± 0.111)	0.853 (± 0.110)	1.326 (± 0.107)	1.054 (± 0.222)
	R.P.	52.9	− 0.239 (± 0.093)	0.906 (± 0.102)	1.138 (± 0.064)	0.802 (± 0.162)
	S.R.	49.1	− 0.121 (± 0.052)	0.813 (± 0.062)	1.104 (± 0.160)	0.771 (± 0.147)
	M.M.	48.2	− 0.129 (± 0.043)	0.773 (± 0.049)	1.107 (± 0.168)	0.668 (± 0.152)
Sedentary	B.B.	42	− 0.127 (± 0.059)	0.952 (± 0.063)	0.948 (± 0.058)	0.712 (± 0.073)
	M.W.	41.8	− 0.218 (± 0.058)	1.136 (± 0.095)	0.792 (± 0.056)	0.684 (± 0.111)
	R.M.	37.5	− 0.125 (± 0.061)	1.141 (± 0.106)	0.741 (± 0.035)	0.575 (± 0.115)
	B.P.	26.6	− 0.090 (± 0.051)	1.662 (± 0.169)	0.397 (± 0.031)	0.562 (± 0.100)

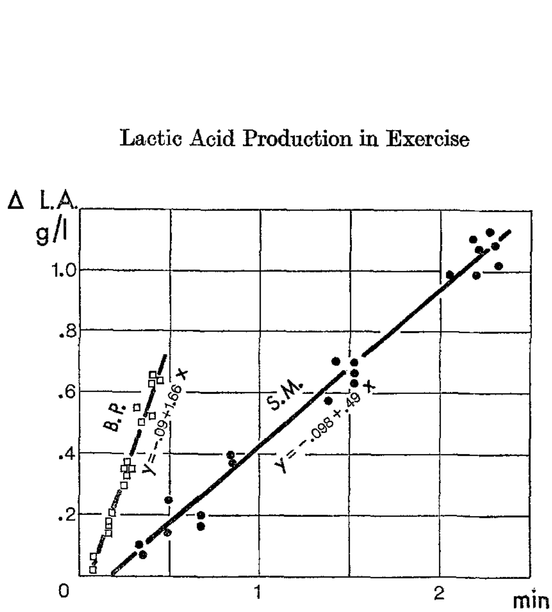

Fig. 1. Lactic acid concentration in blood above the rest value as a function of the duration of the exercise in two subjects, *B.P.*, having a low, and *S.M.* a high maximal aerobic power (see Table)

In Fig. 1 the experiments performed on two subjects are shown as an example. The correlation coefficient of the functions for all subjects has a value ranging from 0.84—0.99. In the Table the values of the constants a and b of eq. (1), as calculated with the method of the least squares are given for all subjects, together with the standard deviation.

The maximal time of performance, together with the maximal blood lactic acid (average of 4 determinations) is also given in the Table. The time of performance runs from a minimum of 28 sec (0.397 min) in subject B.P., to a maximum of 140 sec (2.33 min) in subject F.C., and the maximal lactic acid concentration in blood at exhaustion reaches values from 0.6 to 1.35 g/l; higher values are reached in the more athletic subjects with a higher maximal aerobic power.

By plotting the rate of lactic acid increase, as given by the constant b of the Table, as a function of $\dot{V}_{O_2}^{max}$, a straight line is obtained as expected, according to eq. (2) (Fig. 2): the value of

$$m = \frac{V_{O_2}\,(\text{ml/kg})}{\text{L.A.}\,(\text{g/l})}$$

can be calculated as

$$\frac{1}{0.027} = 37\ (\pm\ 3.5)\ \text{ml of } O_2.$$

Assuming that the distribution of lactic acid in the body fluids is such that the amount of lactic acid in 1 kg of body weight is equivalent to the lactic acid contained in 0.75 l of blood [8], 1 g of lactic acid would correspond to 37/0.75 = 50 ml of O_2 or 250 cal. This value for the O_2 equivalent

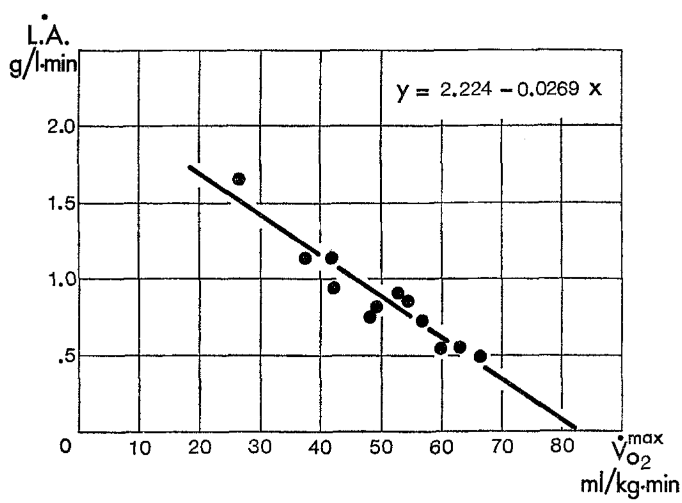

Fig. 2. Rate of increase of lactic acid in blood in g/l · min as a function of the maximal aerobic power expressed in oxygen consumption, ml/kg · min

of L.A. is not too different from that previously found (220 cal/g) [8] thus confirming the validity of the conclusions reached concerning the significance of L.A. production in muscular exercise [8].

The line extrapolated to L.A. = 0 cuts the abscissa at 83 ml of O_2, a value corresponding with sufficient approximation to the O_2 requirement for that work load, or to the maximal O_2 consumption that the subject should have, had he no other available energy source.

The Delayed Formation of L.A. in Supramaximal Exercise

The delayed appearance of lactic acid in supramaximal exercise which has been described earlier [7] is also evident in the present series of experiments. From the data of Fig. 1 and of the Table in fact the delay of the lactic acid appearance is given by the time t_0 at which L.A. = 0. This can be calculated from the constants in the Table as $t_0 = -\frac{a}{b}$. This delay is plotted in Fig. 3 as a function of the maximal $\dot{V}_{O_2}$ for all the subjects. The points are too scattered to allow an exact quantitative treatment: nevertheless it is evident that the general trend is an increase of t_0 with increasing $\dot{V}_{O_2}^{max}$ or, as the work load $\dot{W}$ was kept constant, with decreasing the anaerobic fraction of exercise, $\dot{W} - \dot{V}_{O_2}^{max}$. The delay in L.A. appearance is due to the fact that early in exercise the main energy source is given by phosphagen splitting: only when this mechanism is at, or near, exhaustion does glycogen breakdown to L.A. or oxidations take place.

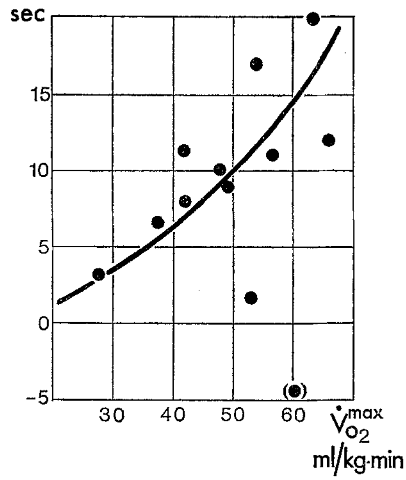

Fig. 3. Delay of increase of blood lactic acid in secs from the beginning of the exercise, as a function of the maximal aerobic power of the subjects

Time Course of the Different Energetic Processes in Supramaximal Exercise

It has been shown earlier that in *submaximal exercise*, no lactic acid is built at steady state [4, 10]. The energy required in this condition is then given by the alactic oxygen debt plus the oxygen actually consumed.

In an exercise involving an energy requirement equal to the *maximum oxygen consumption*, for example 40 ml/kg · min of O_2, the oxygen consumption increases exponentially with a time constant $k = 0.6$ [3, 9] as indicated by the broken line of Fig. 4. The area delimited by this line, the $\dot{V}_{O_2}^{max}$ line, and the ordinate, i.e. the areas indicated by 1 and 2, are indicative of the alactic oxygen debt contracted, which amounts to 28.5 ml/kg. This is also, presumably, the maximum alactic oxygen debt that can be contracted by this individual. As the alactic oxygen debt is paid at the end of the exercise, the energy spent for the performance can be expressed by the oxygen consumption at steady state times the performance time, t, which in Fig. 4 is the area subtended by the $\dot{V}_{O_2}^{max}$ line and the abscissa, i.e. the sum of areas 1, 2 and 5.

When a *supramaximal exercise* however is performed, the fraction of energy required above the maximal aerobic power is supplied by both the lactic acid formation and the alactic mechanism. In fact the oxygen consumption at the onset of exercise increases with the same time constant in all conditions; but the rate of increase is proportional not to the actual net oxygen consumption at the steady state, $\dot{V}_{O_2}^{max}$, but to the energy requirement or the intensity of the exercise, $\dot{W}$, [9]. In supramaximal

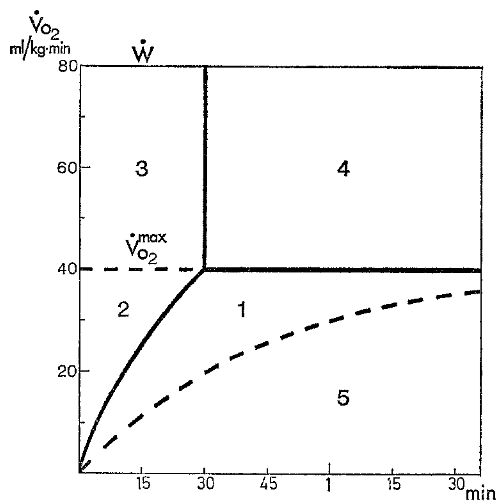

Fig. 4. The three components of energy expenditure ($\dot{W}$), expressed in O_2 equivalent per kg of body weight per min in maximal ($\dot{W} = \dot{V}_{O_2}^{max} = 40$ ml/kg · min) and in supramaximal exercise ($\dot{W} = 80$ ml/kg · min): the areas numbered are representative of the energy contribution of each component (see text)

exercise, involving an energy requirement of 80 ml/kg · min of O_2, the oxygen consumption increases twice as fast, as indicated by the continuous line. The area delimited by this line, the $\dot{V}_{O_2}^{max}$ line and the ordinate (area 2) corresponds to only 8.2 ml of O_2, thus leaving $28.5 - 8.2 = 20.3$ ml of O_2 to cover the supramaximal fraction of the energy required (area 3).

From the description of Fig. 4 it appears that as the oxidative energy sets in progressively at a relatively slow pace, at the very onset of exercise, all the energy requirement is met by the phosphagen breakdown; the contraction of the lactacid oxygen debt is a delayed event, that does not start before a consistent fraction of the phosphagen has been broken down in the muscles [8].

In the case of Fig. 4 at the end of the first 30 secs of work, the oxygen consumption has reached its maximum, and the alactic oxygen debt has been fully contracted. Only then does the lactacid mechanism enter into play, thereby being responsible alone for the supramaximal fraction of the energy expenditure.

On this line a) the delay of the onset of the lactacid mechanism and b) the constant rate of L.A. production in the later part of the exercise (see Figs. 1 and 3) can be visualized: after 30 sec from the start, the energy expenditure is sustained by the lactacid and by the oxidative mechanisms only, as indicated in formula (2) and by the experimental data of the Table and Fig. 2. When the lactacid mechanism is exhausted, the full energy requirement cannot be met any more: the exercise must then come to a stop. In Fig. 4 the capacity of the lactacid mechanism is given by the area numbered 4. This amounts to little more than the energy furnished by the maximal oxygen consumption in 1 min, as it will be shown later.

The description of Fig. 4 is perhaps too schematical, but it gives an approximate picture of the energy processes taking place in the muscles in this condition. It is based on the assumption that all the L.A. found after the exercise has actually been produced during the exercise: this is unlikely, as in supramaximal exercise L.A. production takes place also in the first few seconds of recovery. This means that actually the alactic O_2 debt contracted during exercise is greater than that calculated and that it appears from Fig. 4, while the lactacid O_2 debt contracted is correspondingly less. At the end of the exercise the delayed L.A. production is employed to pay part of the alactic O_2 debt actually contracted during the exercise. The data in Fig. 4 therefore do not describe the real time course of the processes involved, but only the final balance of the alactic and lactacid fractions of the O_2 debt contraction.

The Time of Performance in Supramaximal Exercise as Related with $\dot{V}_{O_2}^{max}$

The total energy spent in a supramaximal exercise can be visualized as being the sum of two components, the *submaximal* and the *supramaximal* energy. These two components are represented in Fig. 4 by the area of the two rectangles separated by the maximum oxygen consumption line, and indicated respect. by the area 1 + 2 + 5, and the area 3 + 4. The supramaximal energy spent during the exercise is given by $t\,(\dot{W} - \dot{V}_{O_2}^{max})$ and this must equal the sum of the energy due to lactic acid (L.A., area 4) expressed in ml of oxygen, plus that fraction of the alactic oxygen debt represented by the area 3, and that can be indicated as P:

$$t\,(\dot{W} - \dot{V}_{O_2}^{max}) = \text{L.A.} + P \tag{3}$$

The capacity of building lactic acid is presumably proportional to the muscular mass, and this may be assumed to be grossly proportional to the maximal oxygen consumption. It is then approximately:

$$\text{L.A.} = n\, \dot{V}_{O_2}^{max} \tag{4}$$

From 3 and (4):

$$\frac{1}{\dot{V}_{O_2}^{max}} = \frac{t + n}{t\dot{W} - P} \tag{5}$$

This equation can be simplified by neglecting P, which is small relatively to $t\dot{W}$ (ab. 15% for the case of Fig. 4):

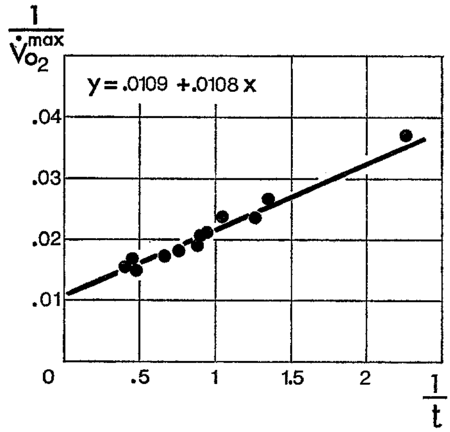

Fig. 5. The reciprocal of the maximal oxygen consumption is plotted as a function of the reciprocal of the duration of the exercise in min as from eq. (6)

$$\frac{1}{\dot{V}_{O_2}^{\max}} = \frac{1}{\dot{W}} + \frac{n}{\dot{W}}\frac{1}{t} \tag{6}$$

It appears then that the reciprocal of the maximum oxygen consumption should be a linear function of the reciprocal of the duration of supramaximal exercise. From the experimental data, this seems to be the case, as shown graphically in Fig. 5. The line cuts the ordinate at a value corresponding to the reciprocal of the total energy requirement, $\frac{1}{\dot{W}}$, and the abscissa at a value corresponding to $-\frac{1}{n}$.

The value of $\dot{W}$, calculated as from eq. (6), bears an error involved in the assumption that P is negligible. It appears that $\dot{W} = \frac{1}{0.0109} = 92$; a value about 15% higher than the actual. On the other hand no error is involved in the calculated value of $n = \frac{\text{L.A.}}{\dot{V}_{O_2}^{\max}} = 0.99$ which is of the same magnitude as previously found [7, 8]: the maximal energy obtained from L.A. formation is about the same as the maximal energy obtained from oxidations in 1 min.

References

1. Edwards, H. T.: Lactic acid in rest and work at high altitude. Amer. J. Physiol. **116**, 367—375 (1936).
2. Gercken, G.: Die quantitative enzymatische Dehydrierung von L (+) Lactat für die Mikroanalyse. Hoppe-Seylers Z. physiol. Chem. **320**, 180—186 (1960).
3. Henry, F. M., De Moor, J.: Lactic and alactic oxygen consumption in moderate exercise of graded intensity. J. appl. Physiol. **8**, 608—614 (1956).

4. Margaria, R.: Aerobic and anaerobic energy sources in muscular exercise. In: Exercise at Altitude, pp. 15—32. Ed. R. Margaria, Amsterdam, Excerpta Medica Foundation 1967.
5. — Aghemo, P., Rovelli, E.: Indirect determination of maximal oxygen consumption in man. J. appl. Physiol. **20**, 1070—1073 (1965).
6. — — — Measurement of muscular power (anaerobic) in man. J. appl. Physiol. **21**, 1662—1665 (1966).
7. — Cerretelli, P., Mangili, F.: Balance and kinetics of anaerobic energy release during strenuous exercise in man. J. appl. Physiol. **19**, 623—628 (1964).
8. — — di Prampero, P. E., Massari, C., Torelli, G.: Kinetics and mechanism of oxygen debt contraction in man. J. appl. Physiol. **18**, 371—377 (1963).
9. — Mangili, F., Cuttica, F., Cerretelli, P.: The kinetics of the oxygen consumption at the onset of muscular exercise in man. Ergonomics **8**, 49—54 (1965).
10. Saiki, H., Margaria, R., Cuttica, F.: Lactic acid production in submaximal muscular exercise. In: Exercise at altitude, pp. 54—57. Ed. R. Margaria. Amsterdam: Excerpta Medica Foundation 1967.

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