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Lactate Kinetics after Short Strenuous Exercise in Man

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Summary. Arterial blood lactate was measured at 10 s time intervals after a 3 min strenuous exercise for six athletes pedaling a bicycle ergometer in the sitting position. Recovery curves were fitted to the equation:

$$Y(t) = A_1(1 - e^{-\gamma_1 t}) + A_2(1 - e^{-\gamma_2 t}) + Y(0) .$$

The evolution of arterial lactate concentrations during recovery can accurately be represented by this equation. The values of the coefficients A and γ found were used for a numerical application to an open two-compartment model: the "working muscle space" (1) and the "lactate space" (2). Intramuscular concentrations, the transfer coefficients from compartment 1 to compartment 2 and from compartment 2 to compartment 1 and the fractional turnover and basal turnover rate were calculated. Computed intramuscular lactate concentrations at the end of exercise compare favorably with those found earlier by muscular biopsic samplings. The turnover data are higher than those previously reported. This discrepancy may possibly be attributed to the method of mathematical analysis.

Key words: Arterial blood lactate – Recovery – Short strenuous exercise – Intramuscular lactate – Compartment analysis.

Blood lactate concentration is generally used in exercise physiology as a measure of anaerobic metabolism, but it reflects only imperfectly the total quantity of lactate produced at the time of exercise. Since the site of lactate production during exercise is the muscular tissue, it would seem more meaningful to measure its muscular concentrations rather than those in the blood. The muscular biopsy technique de-

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scribed in 1962 (Bergström, 1975) allows intramuscular lactate determinations, but its use cannot routinely be applied to man. To the extent that blood lactate concentration decreases as a known function of time during recovery following muscular exercise (Margaria et al., 1933; Margaria and Edwards, 1934; Freund et al., 1972) the indirect determination of intramuscular lactate is possible using a mathematical model. Brodan and Kuhn (1969) thus estimated the approximate total lactate formed during a 6 min submaximal exercise from venous lactate concentrations.

The object of the present work is to set up equations describing the evolution of arterial blood lactate beginning immediately after a short, strenuous muscular exercise of 3 min, to propose a compartmental model accounting for the lactate distribution under such conditions, and finally to estimate the intramuscular lactate concentrations from this model.

Materials and Methods

The experiments were run on six male athletes whose main characteristics are listed in Table 1. The day of the experiment, the subjects arrived at the laboratory at 7 a.m. and had a standard breakfast. A Cournand needle was placed in the humeral artery under local anesthesic and a catheter was inserted in the brachiocephalic vein. Blood clotting was prevented by heparin injection. The needle and the catheter were connected to an automatic analysis system that simultaneously measured venous and arterial lactates and pyruvates. The results were recorded every 10 s during the data collection period on punched tape (Freund, 1970).

The experiment consisted of the following consecutive phases: a 10 min rest, a 10 min submaximal conditioning exercise, a recovery of 30 min, a strenuous exercise of 3 min, and a recovery of 60–70 min. The subjects worked on a bicycle ergometer in a seated position. The workloads imposed were determined beforehand in separate tests. The load for the heavy exercise was chosen in such a manner as to obtain a pulse rate of 170 beats/min^{-1} while pedalling at 60 rpm (PWC 170 according to Wahlund, 1948). The load for the submaximal exercise was half that of the strenuous work.

For the variation of arterial lactate during the recovery period following strenuous exercise, the data obtained for each subject were fitted by the least squares method to the following equation:

$$Y(t) = A_1(1 - e^{-\gamma_1 t}) + A_2(1 - e^{-\gamma_2 t}) + Y(0)\,. \tag{1}$$

The form of Equation 1 allows an interpretation of its parameters, with one exponential function associated with an increase and the other with a decrease in lactate concentration.

Table 1. Main characteristics of the subjects

Subject	Age (years)	Weight (kg)	Height (m)	PWC 170 (W)
C. D.	23	89.5	1.82	230
D. J.	20	70	1.75	230
S. W.	25	74	1.94	320
S. P.	21	79	1.78	270
R. R.	27	74	1.82	250
K. R.	23	71	1.79	200
Mean	23.2	76.3	1.82	250
± SD	2.6	7.2	0.07	41.5

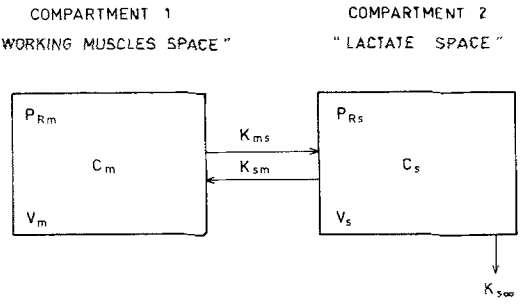

Fig. 1. Open two-compartment system illustrating the exchange of lactate between working muscles and lactate space (see list of abbreviations and symbols)

Mathematical Model

A. Two-Compartment Model

This study was expressly limited to the lactate distribution after a short strenuous muscular exercise. Under such conditions, it is possible to neglect lactate metabolism and diffusion during exercise, and to identify the quantity accumulated in the working muscles at the end of exercise with the total amount produced.

The phenomena of interest here can be illustrated by an open two-compartment system (Fig. 1). One compartment represents the working muscles (here those of the two legs, the "working muscle space"), the other the volume of the remaining body fluids in which the lactate is distributed ("lactate space"). The total lactate space is equal to the sum of the volumes of these two compartments.

Several assumptions were made to allow mathematical solution:

the exchanges between the two compartments are set by the coefficients given in Figure 1;
lactate diffusion is fast within the "lactate space";
lactate leaves the system only through the "lactate space";
the coefficients P_{Rm}, P_{Rs}, K_{sm}, K_{ms}, and $K_{s\infty}$ are constants.

B. Storage Laws

Taking into account the lactate entering and leaving each of the two compartments, the following two first order linear differential equations were set up:

$$\text{Compartment 1: } \frac{dC_m}{dt} = -K_{ms}C_m + K_{sm}\frac{V_s}{V_m}C_s + P_{Rm}\,. \tag{2}$$

$$\text{Compartment 2: } \frac{dC_s}{dt} = -C_s(K_{sm} + K_{s\infty}) + K_{ms}\frac{V_m}{V_s}C_m + P_{Rs}\,. \tag{3}$$

The signs in the equations were chosen so that all constants are positive.

C. Solution of the Differential Equations

The quantity $[K_{ms} - (K_{sm} + K_{s\infty})]^2 + 4\,K_{sm}K_{ms}$ being positive, the solution of the system of differential Equations 2 and 3 shows that the transient behavior of $C_m(t)$ and $C_s(t)$ is a sum of two exponential functions such that:

$$\text{Compartment 1: } C_m(t) = B_1(1 - e^{-\gamma_1 t}) + B_2(1 - e^{-\gamma_2 t}) + C_m(0)\,. \tag{4}$$

$$\text{Compartment 2: } C_s(t) = A_1(1 - e^{-\gamma_1 t}) + A_2(1 - e^{-\gamma_2 t}) + C_s(0)\,. \tag{5}$$

In view of the fast diffusion of lactate within the "lactate space" (second assumption under A. above), the blood lactate concentrations are representative of those in the lactate space, which means that Equations 1 and 5 are equivalent [$C_s(t) = Y(t)$]. Fits to the curves of blood lactate evolution during the recovery period thus allow the evaluation of γ_1 and γ_2 in Equations 4 and 5 as well as of A_1, A_2 and $C_s(0)$ in Equation 5. To determine the coefficients B_1, B_2 and $C_m(0)$ of Equation 4, one can show that

$$\gamma_1 + \gamma_2 = K_{ms} + K_{sm} + K_{s\infty} \tag{6}$$

and

$$\gamma_1\gamma_2 = K_{ms}K_{sm} . \tag{7}$$

Also by differentiating Equations 4 and 5 with respect to time and equating them to Equations 2 and 3, respectively, one obtains

$$B_1 = \frac{K_{sm}V_s}{V_m(K_{ms} - \gamma_1)}A_1 , \tag{8}$$

$$B_2 = \frac{K_{sm}V_s}{V_m(K_{ms} - \gamma_2)}A_2 . \tag{9}$$

Moreover, if $C_m(\infty)$ and $C_s(\infty)$ are the limiting values attained by C_m in compartment 1 and by C_s in compartment 2, respectively, at an infinite time, Equations 4 and 5 yield:

$$C_m(\infty) = B_1 + B_2 + C_m(0) \tag{10}$$

and

$$C_s(\infty) = A_1 + A_2 + C_s(0) . \tag{11}$$

Finally, by letting t approach infinity, the system of Equations 2 and 3 becomes:

$$- K_{ms}C_m(\infty) + K_{sm}\frac{V_s}{V_m}C_s(\infty) + P_{Rm} = 0 , \tag{12}$$

$$K_{ms}\frac{V_m}{V_s}C_m(\infty) - C_s(\infty)(K_{sm} + K_{s\infty}) + P_{Rs} = 0 . \tag{13}$$

Table 2. Summary of the conditions used in each of the hypotheses (see list of abbreviations and symbols)

Hypotheses	Equations used	Theoretical expressions for the calculated parameters
Case I	(6), (7), (12)	$K_{ms} = [\gamma_1 + \gamma_2 + P_{Rm}/(V_{sm}C_s(\infty)) \pm \sqrt{\Delta}]\ V_{sm}/2\ (V_{sm} + 1)$ with $\Delta = [\gamma_1 + \gamma_2 + P_{Rm}/(V_{sm}C_s(\infty))]^1 - 4\ (1 + 1/V_{sm})\gamma_1\gamma_2 \geqslant 0$
P_{Rm} given	(12)	$K_{sm} = K_{ms}/V_{sm} - P_{Rm}/V_{sm}C_s(\infty)$
$C_m(\infty) = C_s(\infty)$	(7)	$K_{s\infty} = \gamma_1\gamma_2/K_{ms}$
	(13)	$P_{Rs} = C_s(\infty)(K_{sm} + K_{s\infty}) - K_{ms}C_s(\infty)/V_{sm}$
Case II	(7)	$K_{ms} = \gamma_1\gamma_2/K_{s\infty}$
	(6)	$K_{sm} = \gamma_1 + \gamma_2 - K_{ms} - K_{s\infty}$
P_{Rm} given	(12)	$C_m(\infty) = [P_{RM} + K_{sm}V_{sm}C_s(\infty)]/K_{ms}$
$K_{s\infty}$ given	(13)	$P_{Rs} = C_s(\infty)(K_{sm} + K_{s\infty}) - K_{ms}C_m(\infty)/V_{sm}$
Case III	(7)	$K_{ms} = \gamma_1\gamma_2/K_{s\infty}$
	(6)	$K_{sm} = \gamma_1 + \gamma_2 - K_{ms} - K_{s\infty}$
$C_m(\infty) = C_s(\infty)$	(13)	$P_{Rs} = C_s(\infty)(K_{sm} + K_{s\infty} - K_{ms}/V_{sm})$
$K_{s\infty}$ given	(12)	$P_{Rm} = K_{ms}C_s(\infty)(1 - V_{sm})$

Of the nine unknowns appearing in Equations 6–10, 12, and 13, six [V_m, V_s, $C_s(\infty)$, P_{Rm}, $K_{s\infty}$, and $C_m(\infty)$] can be estimated from the present and other results. For the remaining three unknowns, hypotheses covering the three pairs of values P_{Rm}, $K_{s\infty}$; P_{Rm}, $C_m(\infty)$ and $K_{s\infty}$, $C_m(\infty)$ can be formulated. In Table 2, together with the differential equations for each hypothetical pair, are presented the expressions of the parameters and, when pertinent, the physical conditions necessary for their solution. If these conditions are not satisfied, the corresponding hypothesis must be rejected.

Results

The observed evolutions of blood lactate concentration are presented in Figure 2 as a function of time for the six subjects during the 5 min preceding exercise, during the 3 min of work, and the subsequent recovery. On the same figure are also presented the curves obtained by fitting Equation 1 to the experimental values during recovery.

These curves all show a similar pattern, the maximum value being reached between the second and the fifth minute of recovery. The standard deviations between

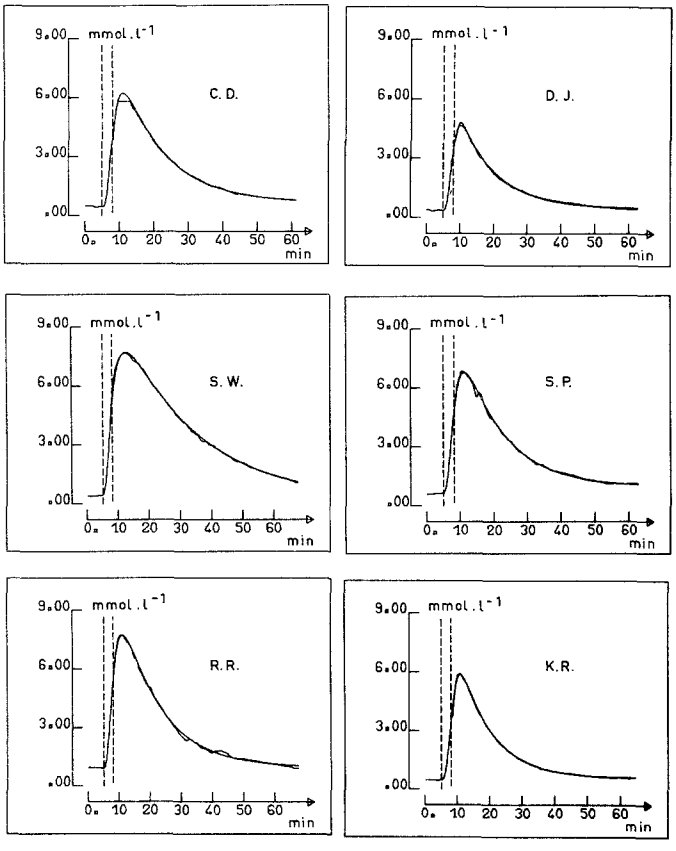

Fig. 2. Evolution of individual blood lactate concentrations before, during and after a 3-min strenuous exercise and fits to experimental data. The dashed vertical lines locate the working period

Table 3. Characteristics of the experimental and fitted curves (see list of abbreviations and symbols)

Subject	Y_i $\mu mol \cdot l^{-1}$	$Y(0)$ $\mu mol \cdot l^{-1}$	Y_{max} $\mu mol \cdot l^{-1}$	γ_1 min^{-1}	γ_2 min^{-1}	γ_1/γ_2	A_1 $\mu mol \cdot l^{-1}$	A_2 $\mu mol \cdot l^{-1}$	$Y(\infty)$ $\mu mol \cdot l^{-1}$	SD $\mu mol \cdot l^{-1}$
C. D.	462	3,687	6,375	0.622	0.0767	8.1	4,939	− 7,992	634	104
D. J.	369	3,275	4,822	0.981	0.0896	10.9	2,665	− 5,491	449	53
S. W.	426	5,359	7,701	0.395	0.0401	9.9	4,816	− 9,979	196	50
S. P.	638	4,531	6,871	0.527	0.0802	6.6	5,192	− 8,763	960	44
R. R.	923	5,258	7,745	0.507	0.0797	6.3	5,910	−10,200	968	84
K. R.	475	3,730	5,900	0.762	0.099	7.7	4,455	− 7,622	563	22
Average	549	4,307	6,569	0.632	0.0776	8.3	4,663	− 8,341	628	–
± SD	204	877	1,122	0.211	0.0201	1.8	1,093	1,737	300	–
Average curve	549	4,613	6,508	0.690	0.0704	9.9	3,768	− 7,647	734	20

the experimental and the fitted curves are small (Table 3) except for subject C.D., for whom the peak of the experimental curve was flattened by a technical incident during the measurements. The value of the standard deviation is approximately 8% of the mean lactate concentration before exercise or 0.8% of the maximum concentration observed during recovery.

The lactate evolution during the whole recovery period can thus be fully represented by a combination of two exponential terms. The values of the coefficients calculated for each of the subjects are given in Table 3, where are also given the values of the parameters of the curve fitted to the averaged data of the six subjects.

Application of the Model

The values of the coefficients A and γ found have been used for a numerical application of the model (Table 2 and Eq. 8–10). For reasons considered below in the discussion, we have taken (inasmuch as their values had to be imposed):

$$V_S = 28.6\ \text{l}, \quad V_m = 13.5\ \text{l}, \quad P_{Rm} = 2\ \mu\text{mol} \cdot \text{l}^{-1} \cdot \text{min}^{-1},$$

$$BTR = 15\ \mu\text{mol} \cdot \text{kg}\ (BM)^{-1} \cdot \text{min}^{-1}, \text{ and } C_m(\infty) = C_s(\infty).$$

The six individual curves as well as the average curve have been treated according to the three hypothetical situations of Table 2. The resolution of the corresponding equations for these three cases leads to the following results for all the curves:

first hypothesis: two possible solutions (depending on the sign before $\sqrt{\Delta}$),

second hypothesis: one possible solution but for $K_{sm} < 0$ and $C_m(\infty) < 0$,

third hypothesis: one possible solution but for $K_{sm} < 0$ and $P_{Rs} < 0$.

The quantities $C_m(\infty)$, K_{sm} and P_{Rs} must be positive from the adopted sign convention. The second and the third cases do not fulfill these conditions and must consequently be excluded, even though $K_{s\infty}$ has been estimated from the BTR of 15 $\mu\text{mol} \cdot \text{kg}\ (BM)^{-1} \cdot \text{min}^{-1}$ proposed by Minaire (1973). For the first case, the two values of K_{ms} give two values for each coefficient (Table 2). To the solution $\sqrt{\Delta}$ correspond:

A high $K_{s\infty}$ which would give a BTR at rest of approximately 170 $\mu\text{mol} \cdot \text{kg}\ (BM)^{-1} \cdot \text{min}^{-1}$ whereas literature values (Minaire, 1973) are of the order of 15 $\mu\text{mol} \cdot \text{kg}\ (BM)^{-1} \cdot \text{min}^{-1}$.

A much too high $C_m(0)$ [intramuscular concentration of lactate at the end of the exercise of 100–120 $\text{mmol} \cdot \text{kg}^{-1}$ wet muscle in contrast to literature values of 16–26 $\text{mmol} \cdot \text{kg}^{-1}$ wet muscle for almost similar experimental conditions (Table 4)].

The differential Equations 2 and 3 thus possess only one solution for which the different parameters take on meaningful values. Table 5 presents these results. The amplitudes B_1 and B_2 of the two exponentials of the expression for $C_m(t)$ are both negative, expressing the fact that the concentration decreases regularly in function of time in the muscle compartment after exercise. Figure 3 represents the computed evolution of intramuscular lactate as compared to observed blood lactate evolution during recovery (average curve).

Table 4. Literature muscular lactate concentrations after maximal exercise from measurements on biopsic samplings

Reference	Lactate mmol · kg^{-1} wet muscle
Diamant et al. (1968)	19.1
Karlsson and Saltin (1970)	16.1
Karlsson (1971a)	17.1
Karlsson (1971b)	23.9
Karlsson (1971c)	17.8
Karlsson and Saltin (1971)	22.5–23.2
Karlsson et al. (1971)	22.7
Karlsson et al. (1972)	14.8–19.3
Knuttgen and Saltin (1972)	18.1
Linnarson et al. (1974)	25.7

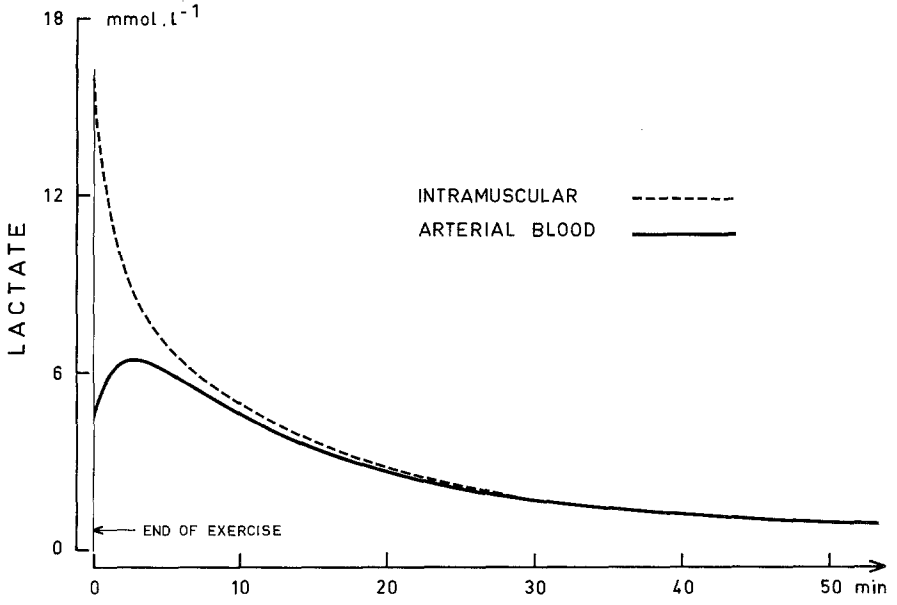

Fig. 3. Intramuscular and arterial blood lactate removal curves during recovery following a 3 min strenuous exercise. Intramuscular concentrations were computed from the values of the parameters A and γ of the curve fitted to the averaged data of the six subjects

Discussion

The curves presented in Figure 2 are similar to those described previously by several authors (Margaria et al., 1933; Margaria and Edwards, 1934; Asmussen, 1950; Davies et al., 1970 etc.) nevertheless they constitute a much more rigorous description of the evolution of blood lactate concentrations during recovery since they were obtained from data measured every 10 s.

In 1933 Margaria et al. showed that the lactate decreased monoexponentialy starting with the sixth minute of recovery. Newman et al. (1936), Johnson and Brouha (1942) and more recently Davies et al. (1970) studied the factors that modify the rate of lactate removal as calculated from the slowly decreasing part of the recovery curve. Nevertheless Forbath et al. (1967) observed in dogs that the decrease in lactate after the injection of ^{14}C labeled L-lactate was not monoexponential. They concluded that the lactate was distributed according to a two- or multicompartmental model. De Coster et al. (1969) thought that because of the complexity of the mechanisms coming into play, one or two exponential terms could not describe the lactate evolution during recovery. However, our results show that a combination of two exponential functions represents accurately the lactate kinetics over the whole recovery period. It is very likely that the phenomena described by these two exponential terms are much more complex. One can conceive that to a first approximation they describe a multiexponential (hence multicompartmental) system where the velocity constants fall into two groups of the same magnitudes as those determined here.

The value of the ratio γ_1/γ_2 (9.9 for the average curve) can be used to estimate γ_1, since its direct determination from the points immediately after the end of the exercise is difficult. The determination of γ_2 is easier because it can be measured on the slowly decreasing part of the curve. Then using the relationship $\gamma_1 = 10\ \gamma_2$, an estimation of γ_1 is feasible and leads to a realistic profil of the lactate evolution starting at the end of the exercise [A_1 can itself be determined from A_2, $Y(\infty)$ and $Y(0)$].

The proposed model cannot be compared with that of Brodan and Kuhn (1969) who supposed that the lactate was distributed uniformly throughout the total water space and that lactate metabolism was negligible during a moderate exercise of 6 min. This may not be a good approximation since the liver (Rowell et al., 1966), the muscles (Jorfeldt, 1970) and other organs (Knuttgen, 1971) utilize lactate during muscular exercise. It seems in addition that the number of samples taken by Brodan and Kuhn during their experiment is insufficient to rigorously determine the form of an equation describing the lactate evolution.

As Knuttgen (1971) emphasized, knowledge of the distribution volume is a critical point in all methods estimating lactate production from blood concentration data. In our model, the volume of the active muscle group, the muscles of the legs, was evaluated as 13.5 l for a body weight of 76 kg. This takes into account a muscle mass of 14—14.5 kg of wet muscle.

The literature values of the total lactate space are controversial. Searle and Cavalieri (1972) evaluated it as 49.4% of the body mass (or as 3/4 of the total water space). Brodan and Kuhn (1969), Kreisberg et al. (1970), and Hermansen and Stensvold (1972) considered that it might be the total water space. Rowell et al. (1966) used a uniform distribution in 50% of the body mass. Ahlborg et al. (1976) found that the lactate was distributed in a volume equal to 34% of the body mass. In our study V_s was estimated as 28.6 l (or 37.7% of the average mass of the subjects). The ratio V_s/V_m is thus equal to 2.1 and the total lactate space to 42.1 l (55% of the average mass of the subjects).

Hagenfeldt (1972) showed that the production in forearm muscle at rest was 2 $\mu mol \cdot l^{-1} \cdot min^{-1}$ muscle. By analogy, this value was assigned to P_{Rm} in two of our

Table 5. Values of the coefficients computed in the numerical application of the open two-compartment model for lactate distribution (see list of abbreviations and symbols)

Subject	K_{ms} min^{-1}	K_{sm} min^{-1}	$K_{s\infty}$ min^{-1}	P_{Rs} $\mu mol \cdot l^{-1} min^{-1}$	B_1 $\mu mol \cdot l^{-1}$	B_2 $\mu mol \cdot l^{-1}$	$C_m(0)$ $\mu mol \cdot l^{-1}$	$C_m(0)$ $\mu mol \cdot kg^{-1}$	$C_m(\infty) = C_s(\infty)$ $\mu mol \cdot l^{-1}$	BTR $\mu mol \cdot kg^{-1} min^{-1}$
C. D.	0.3916	0.1850	0.129	76.25	−8,338	− 9,850	18,830	17,850	634	30.8
D. J.	0.6322	0.2989	0.139	61.41	−4,804	− 6,353	11,610	11,000	449	23.5
S. W.	0.2563	0.1172	0.062	11.18	−8,533	−11,359	20,090	19,040	196	4.6
S. P.	0.3233	0.1530	0.131	124.50	−8,199	−11,580	20,740	19,660	960	47.4
R. R.	0.3094	0.1464	0.130	125.30	−9,215	−13,645	23,830	22,590	968	47.4
K. R.	0.4773	0.2256	0.158	88.00	−7,415	− 9,545	17,520	16,610	563	33.5
Average	0.3984	0.1877	0.125	81.11	−7,751	−10,389	18,770	17,792	628	31.2
± SD	0.1376	0.0659	0.033	42.86	1,555	2,460	4,100	3,888	300	16.1
Average curve	0.4414	0.2089	0.110	79.80	−6,651	− 9,040	16,430	15,570	734	30.4

three hypotheses. In addition, for our calculations, we have assumed that in an organism in metabolic equilibrium, the lactate concentration in tissue water is equal to that of the plasma. Considering that tissue represents 77% of the mass of wet muscle (Karlsson, 1971) and that the density of wet muscle is 1.055, and taking into account that our analyses were performed on whole blood and consequently that to obtain plasma concentrations, blood concentrations are to be divided by about 0.8, the relationship between $C_m(\infty)$ and $C_s(\infty)$ at infinite time can be written:

$$\text{for } t \to \infty \, C_s(\infty)/0.8 = C_m(\infty)/0.77 \times 1.055$$

where $C_s(\infty)$ is expressed in $\mu mol \cdot l^{-1}$ blood and $C_m(\infty)$ in $\mu mol \cdot kg^{-1}$ wet muscle. To a good approximation, the limiting condition $C_s(\infty) = C_m(\infty)$ for a muscle at rest can thus be used.

For the relationship between $K_{s\infty}$ and the *BTR* of lactate we have taken:

$$BTR = K_{s\infty} \times C_s(\infty) \times V_s/BM$$

since according to Depocas et al. (1969) and Freminet et al. (1972), there is a linear relationship between the turnover rate and the plasma lactate concentration. Ahlborg et al. (1976) reported during intravenous lactate infusion, a fractional turnover of 0.076 min^{-1} corresponding to a *BTR* of $14 \cdot 2$ $\mu mol \cdot min^{-1} \cdot kg\ (BM)^{-1}$ for a lactate concentration at rest of 0.550 $mmol \cdot l^{-1}$. Kreisberg et al. (1972) and Searle and Cavalieri (1972) observed a turnover rate of respectively 15 and 18 $\mu mol \cdot min^{-1} \cdot kg\ (BM)^{-1}$ after injection or infusion of ^{14}C labelled lactate. The turnover data calculated with our model are higher (Table 5). The differences may be due to the fact that our estimations have been made after muscular exercise. They may also be related to our mathematical model or to the assumptions needed to solve the equations.

The intramuscular lactate concentrations at the end of the exercise calculated with the model are very close to those found by other authors in analogous experimental situations. For five of the six subjects, this value is between 16 and 23 $mmol \cdot kg^{-1}$ wet muscle. The values found by biopsic muscle punctures after maximal exercises are between 16 and 26 $mmol \cdot kg^{-1}$ wet muscle (Table 4).

Certainly all the intervening physiological processes are not included in the model. Among other factors, variations of the local and the general circulatory rate, of the plasma and muscle volumes, and lactate uptake by the working muscles have not been taken into account.

However, the model we are proposing allows the calculation to a satisfactory approximation of the total lactate accumulated in the working muscles at the end of an exercise. In addition, it allows the estimation of the fractional turnover and consequently of the basal turnover rate of lactate, and of the exchange coefficients between working muscles and the "lactate space". These reasons alone would fully justify the use of the model to study factors likely to modify these coefficients, such as physical training, altitude, hypoxia, active recovery or ambient temperature.

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List of Abbreviations and Symbols

A_1, A_2	Amplitudes of the two exponential terms fitted on the arterial lactate concentrations ($\mu mol \cdot l^{-1}$)
B_1, B_2	Amplitudes of the two exponential terms of the intramuscular lactate concentrations ($mol \cdot l^{-1}$)
BM	Body mass
BTR	Basal turnover rate of the lactate pool calculated from the relationship: $BTR = K_{s\infty} \times C_s(\infty) \times 0.377$ ($\mu mol \cdot kg\ (BM)^{-1} \cdot min^{-1}$)
$C_m(t)$	Lactate concentration in the "working muscle space" at time t ($\mu mol \cdot l^{-1}$ wet muscle)
$C_s(t)$	Lactate concentrations in the "lactate space" at time t ($\mu mol \cdot l^{-1}$)
γ_1, γ_2	Velocity constants of the fitted exponential terms (min^{-1})
K_{ms}	Transfert coefficient from the "working muscle space" to the "lactate space" (min^{-1})
K_{sm}	Transfert coefficient from the "lactate space" to the "working muscle space" (min^{-1})
$K_{s\infty}$	Fractional turnover of lactate (min^{-1})
P_{Rm}	Lactate production in the "working muscle space" $\mu mol \cdot l^{-1} \cdot min^{-1}$
P_{Rs}	Lactate production in the "lactate space" $\mu mol \cdot l^{-1} \cdot min^{-1}$
t	Time after the end of exercise (min)
V_m	Volume of the "working muscle space" (l)
V_s	Volume of the "lactate space" (l) [37.7% of the body mass]
$V_{ms} = V_m/V_s$	
Y_i	Pre-exercise arterial lactate concentration ($\mu mol \cdot l^{-1}$)
Y_{max}	Arterial lactate peak value during recovery ($\mu mol \cdot l^{-1}$)
$Y(t)$	Arterial lactate concentration at time t ($\mu mol \cdot l^{-1}$)

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