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Oxygen deficit and debt in submaximal exercise at sea level and high altitude

J. RAYNAUD, J. P. MARTINEAUD, J. BORDACHAR, M. C. TILLOUS, AND J. DURAND
Departement de Physiologie Humaine, UER Kremlin-Bicêtre, Centre Chirurgical Marie Lannelongue, 75013, Paris, France; and Instituto Boliviano de Biologia de Altura, La Paz, Bolivia

Raynaud, J., J. P. Martineaud, J. Bordachar, M. C. Tillous, and J. Durand. *Oxygen deficit and debt in submaximal exercise at sea level and high altitude.* J. Appl. Physiol. 37(1): 43–48. 1974.—Kinetics of O_2 uptake ($\dot{V}O_2$) during exercise (3 work loads, 2 time periods) show that for a given work load O_2 deficit is larger at high altitude (HA) than at sea level (SL). However, the relationship between deficit and percent of maximal O_2 uptake ($\dot{V}O_{2\,max}$) remains unchanged because $\dot{V}O_{2\,max}$ is reduced by about 15% at HA. Oxygen debt increases with intensity and duration of work. It is always larger than the deficit. Under any conditions of work load and duration, debt is smaller at HA than at SL. The fast components of deficit and debt are linearly related to exercise steady-state $\dot{V}O_2$ by the same ratio; this ratio is unaffected at HA. So debt is higher than deficit due to its slow component. Unexpectedly, a smaller slow component is accompanied at HA by a higher lactic acid concentration. It was shown (*J. Appl. Physiol.* 34: 633–638, 1973) that body heat storage during exercise and recovery is reduced in subjects translocated to HA; this result suggests that temperature affects magnitude of the slow component of the debt.

lactic acid; maximal O_2 uptake

The time course of the two complementary energy sources, creatine phosphate stores and anaerobic glycolysis, which compensate for O_2 deficiency at onset of exercise, has been studied directly and indirectly. Kinetics of O_2 uptake ($\dot{V}O_2$) prior to steady state can be described by one single exponential with a short time constant for moderate work. Two exponentials are necessary for workloads higher than 50% of maximal O_2 uptake ($\dot{V}O_{2\,max}$) (9, 13, 35). These findings indirectly suggest that initial O_2 deficit is made up of two components. Final O_2 debt also was decomposed into a fast component and one or two slow components according to the intensity and duration of exercise (20, 23).

The nature of the fast component of O_2 deficit and O_2 debt has been extensively studied by directly analyzing the time sequence of muscular creatine phosphate concentration at the beginning and end of muscular exercise in dog (25, 26) and in man (15, 17). The results obtained by the different authors agree in that the time constant of splitting and restoring creatine phosphate stores equals about 0.45 min. Interpretations of the slow components of deficit and debt are more questionable. The time sequence of anaerobic glycolysis at the beginning of work is still hypothetical (28, 29); the connection of lactic acid (LA) metabolism with O_2 uptake during recovery presently is a matter of controversy (4, 12, 18, 22).

This study was designed to follow $\dot{V}O_2$ changes at onset and offset of exercise, in order to compare by indirect method the relative role played by the two creditors of complementary energy at sea level (SL) and high altitude (HA).

Subjects and Methods

Three subjects were studied comparatively at SL (Paris: 50 m; P_B: 761 Torr) and after 3 wk at HA (La Paz: 3,800 m; P_B: 494 Torr). They were untrained physicians, two males and one female, aged from 37 to 43 yr, characterized by the following height and weight: *PM*—1.75 m, 72 kg; *JPM*—1.74 m, 65 kg; *JR*—1.62 m, 49 kg.

A 30-min rest period, while the subject sat on the bicycle, preceded exercise. Exercise was performed on a bicycle ergometer (Minjhart type) at a pedaling frequency of 60 rpm at three different work loads for two durations, 10 and 25 min. Each test was performed twice. Work load and duration were chosen randomly at a rate of one type of exercise on each day. Work loads for *subjects JPM* and *PM* were 60, 120, and 150 W and for *subject JR* 40, 60, and 80 W. To save time because of the brief sojourn at altitude, experiments were carried on in the morning and the afternoon but the time of the day was the same for each subject at SL and HA.

The subject breathed through a mouthpiece. The expiratory valve was connected to a two stopcock device so that the expired gases could be collected in Douglas bags. The bag collections were for 1-min periods during the first 10 min of exercise and the first 5 min of recovery and for 2- and 5-min periods during the remainder of the work and recovery, respectively. The recovery period lasted 50 min; the return to rest $\dot{V}O_2$ value was obtained in every case. Gas analysis was performed using an infrared analyzer for CO_2 (Cosma, type 80) and paramagnetic for O_2 (Servomex). The volume of the bags was measured in a Tissot spirometer and corrected for the volume taken by the analyzers. The apparatus (bicycle, analyzers) were identical at SL and HA. Oxygen uptake was calculated by open-circuit method. ECG was continuously recorded.

Maximal O_2 uptake was determined by Maritz's indirect method (24) knowing the linear relationship between heart rate (HR) and $\dot{V}O_2$ and the maximal HR (HR_{max}) for each subject. Theoretical HR $_{max}$ according to age was deduced from data reported by Asmussen (2). The equation of the slope was calculated and HR $_{max}$ was obtained by solving the equation for the age in the three subjects. Validity of this estimation will be discussed later. Maximal HR at HA was taken as equal to HR $_{max}$ at SL minus 10, according to data reported by different authors (10, 21, 30), the magnitude of the reduction being independent of physical fitness.

Initial O_2 deficit was computed by adding the sequential differences between steady-state $\dot{V}o_2$ ($\dot{V}o_{2\ st\text{-}st\ ex}$) and actual $\dot{V}o_2$ measured every min during transient phase. The mean values of $\dot{V}o_2$ during the last 2 min of work in 10-min exercises and the last 10 min in 25-min exercises were taken as $\dot{V}o_{2\ st\text{-}st\ ex}$ values. Final O_2 debt was computed as the sum of the differences between actual sequent $\dot{V}o_2$ measured during recovery and rest $\dot{V}o_2$. Rest $\dot{V}o_2$ was determined three times during 5-min periods; the mean value of the three determinations was taken as rest reference. The 1st min of deficit and debt was considered as representative of the fast component. Such an estimation is arbitrary, based on results reported by different authors (17, 25, 29) and will be discussed. The slow component was estimated as the difference between total value and value of the 1st min.

Blood samples were drawn for [LA] determinations during the 25-min exercise performed at the highest work load only. For these tests, an indwelling catheter was inserted into a brachial vein during the previous rest period. Sampling time is indicated on Fig. 8. Determinations of plasma [LA] were made by enzymatic technique using Boeringher test kits. Blood samples drawn during exercise at HA were centrifuged in La Paz and plasma was sent by air in liquid nitrogen containers to Paris where analyses were performed. A previous study shows that storage in liquid nitrogen does not alter plasma [LA] measurements.

RESULTS

Mean values were calculated with six individual data and reported ± 1 SE.

Steady-state data. Rest $\dot{V}o_2$ is significantly higher at HA than at SL (SL: 136 $\pm$ 3 $ml \cdot min^{-1} \cdot m^{-2}$; HA: 145 $\pm$ 3; $P > 0.02$). Heart rate is closely related to $\dot{V}o_2$ increase (SL: 69 $\pm$ 1 $beats \cdot min^{-1}$; HA 80 $\pm$ 1; $P > 0.001$).

However, $\dot{V}o_{2\ st\text{-}st\ ex}$ is identical at SL and HA for the same mechanical work load. Figure 1 depicts the relationship between $\dot{V}o_{2\ st\text{-}st\ ex}$ and mechanical power at SL and HA. The slopes are not significantly different. The intercept on the ordinate is higher than rest $\dot{V}o_2$ because it probably corresponds to $\dot{V}o_2$ at unloaded exercise.

Heart rate at steady state of exercise was plotted against corresponding $\dot{V}o_2$. The relationship in each case is linear as illustrated by Fig. 2. The intercept with the ordinate is always higher at HA but the incline is quite similar. Maximal $\dot{V}o_2$ at SL and HA was calculated for each subject by solving the equations of Fig. 2 for the respective values of HR_{max} ($\dot{V}o_{2\ max}$, $ml \cdot min^{-1}$ at SL and HA: *PM*—3,150, 2,580; *JPM*—2,270,1,900; *JR*—1,700,1,450). Relative work load ($\dot{V}o_{2\ st\text{-}st\ ex}$ $100/\dot{V}o_{2\ max}$) could be deduced from these data.

Transient phases data. Figure 3 shows the different values of total deficit plotted as a function of relative work load. The points at SL and HA cannot be differentiated. As the total deficit has been decomposed into two components, the heavy line of Fig. 3 is the graph representing the sum of the fast and slow component as a function of relative workload.

The 1st min deficit, which is assumed to be an index of the fast component, follows a linear relationship with the equation indicated by a dashed line on Fig. 3 when plotted against relative work load. The relationship is unchanged at altitude. However, the slope has no clear physiological meaning because relative work load is a ratio. The individual 1st min deficit plotted against the corresponding $\dot{V}o_{2\ st\text{-}st\ ex}$ also exhibits a linear relationship shown on Fig. 4. The regression coefficient is much better in this case (0.94) than in the previous relationship (0.82). The slope has the dimension of time and has the same value at SL and

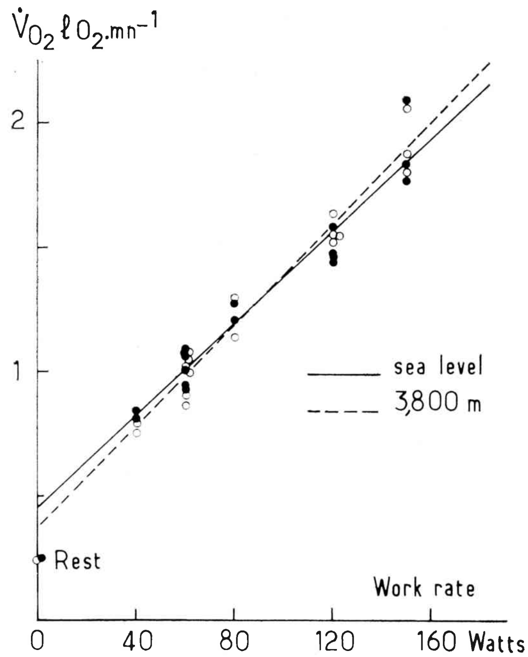

FIG. 1. Oxygen uptake at steady-state exercise as a function of mechanical power (SL: ●; HA: ○). Two slopes are not significantly different. Intercept represents $\dot{V}o_2$ for unloaded exercise.

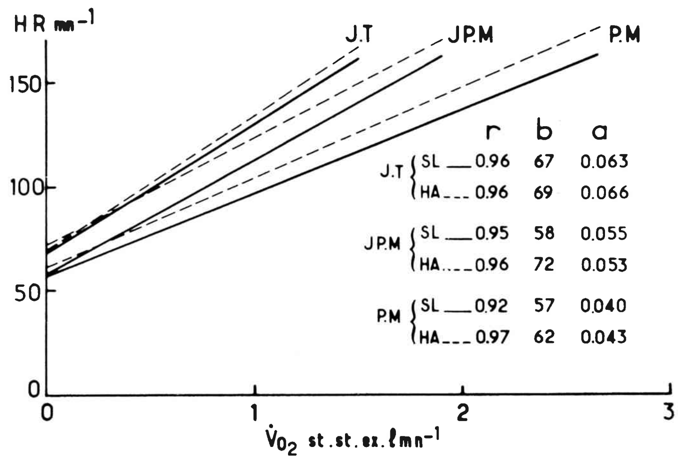

FIG. 2. Heart rate at steady-state exercise for different work loads is plotted against respective $\dot{V}o_{2\ st\text{-}st\ ex}$. Equations at SL and HA are reported for every subject. Slope *a* is very similar at SL and HA. Intercept *b* is always higher at HA; *r* is regression coefficient.

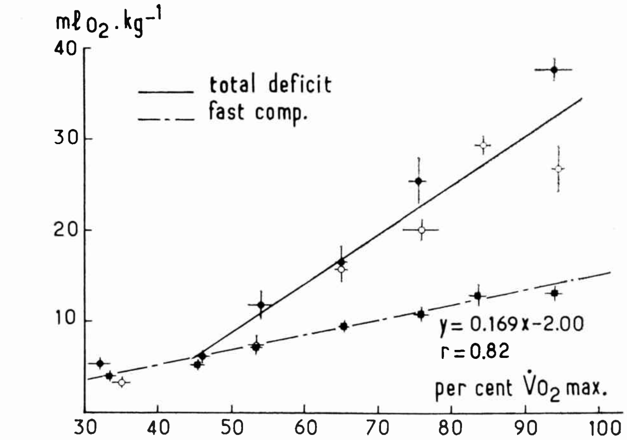

FIG. 3. Total deficit at SL (●) and HA (○) is plotted against percent of $\dot{V}o_{2\ max}$. Dashed line represents graph of the relationship of 1st min deficit at SL and HA versus percent of $\dot{V}o_{2\ max}$. Mean points ($\pm$ SE) were calculated from data included within intervals of 10% of $\dot{V}o_{2\ max}$. Heavy line is graph resulting in adding slope of slow component (Fig. 5).

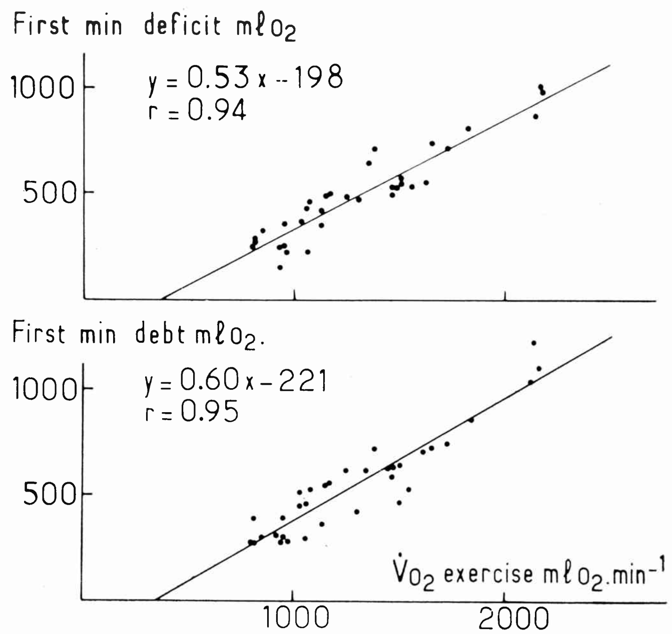

FIG. 4. Actual values of 1st min deficit and debt which are assumed to be an index of the fast component of deficit and debt are plotted against $\dot{V}o_{2\ st\text{-}st\ ex}$. The above slopes are defined by data obtained at SL. At HA, following equations are obtained: 1st min deficit: $y = 0.54$ min, $r = 0.95$; 1st min debt: $y = 0.60$ min, $r = 0.9$. Slope and intercept at HA are identical to those obtained at SL.

HA (SL: 0.53 min; HA: 0.54). The slow component of the deficit, as was previously defined, though more scattered is also linearly related to relative work load (Fig. 5); the slopes at SL and HA are not different.

In Fig. 6 total debt of 10-min exercise at SL and HA is plotted against percent of aerobic capacity. The mean points at SL describe a curvilinear relationship and are always situated above points at HA. Figure 7 shows that the curves at SL and HA deviate from each other much more for 25-min exercises. In any case, debt values exceed those of deficit. The scattering of debt values is larger than those of deficit because the experimental data are four times less

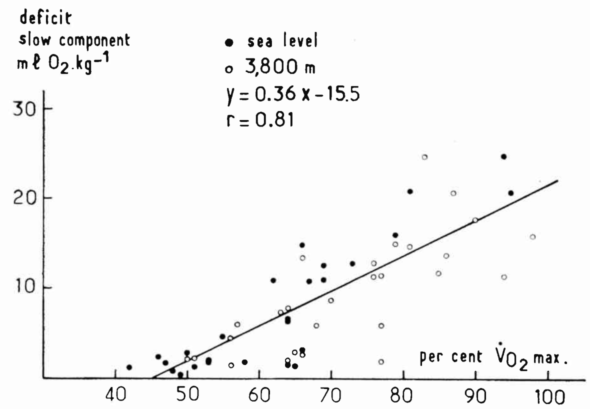

FIG. 5. Deficit slow component was determined by subtracting 1st min deficit from total deficit. Individual data are reported on graph. Intercept indicates anaerobic threshold which appears at about 45% of $\dot{V}o_{2\ max}$ at SL (●) and HA (○).

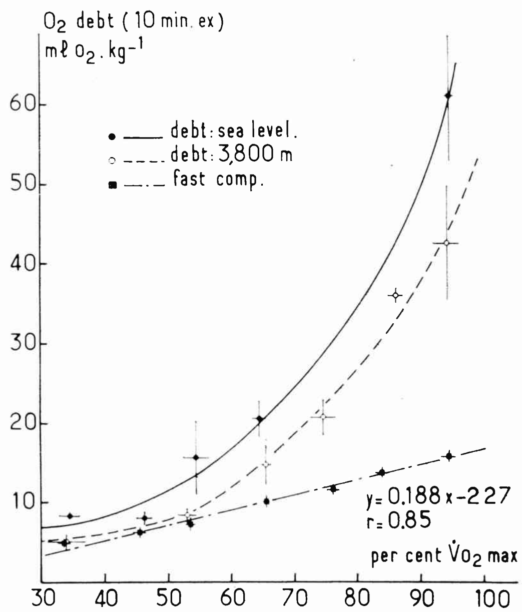

FIG. 6. Total debt at SL and HA in 10-min exercise. Dashed line is graph of relationships of 1st min debt versus relative work load. Points are means $\pm$ SE of values included within intervals of 10% of $\dot{V}o_{2\ max}$. Comparison with Fig. 3 shows that debt is higher than deficit; however, the discrepancy is not obvious for mild exercise. Debt is always smaller at HA than at SL.

numerous than those of deficit. Also estimation of debt is less accurate for at least two reasons. First, $\dot{V}o_2$ measurement after 20 min of recovery exceeds rest $\dot{V}o_2$ by only a few milliliters. However, this small extra $\dot{V}o_2$ has an important effect on the calculation of total O_2 debt because it is integrated for a long time. Obviously any cause of discomfort for the subject, which necessarily increases $\dot{V}o_2$ during this lengthy recovery, induces error in the determination of O_2 debt. Therefore, recovery was set up to 50 min in all experiments even at weak work loads. Second, the smaller the $\dot{V}o_2$ values, the greater the importance of the relative error of experimental measurements. It can be said that at SL total debt increases not only with intensity but also with duration of exercise. At HA these relationships are found again, but for given conditions of work load and duration

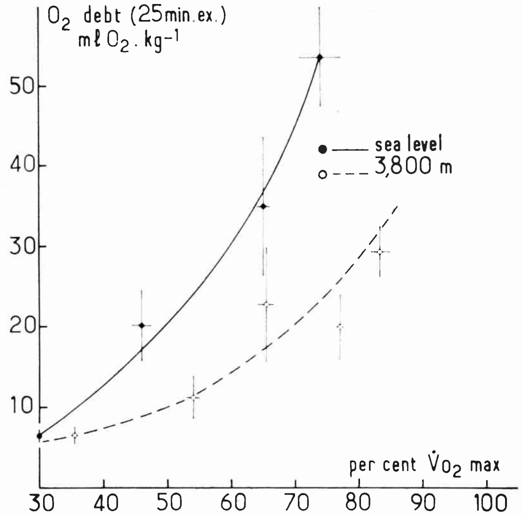

FIG. 7. Total debt at SL and HA in 25-min exercise. Comparison with Fig. 6 shows that debt increases with duration of work. Difference between SL and HA curves is much more obvious than in 10-min exercise.

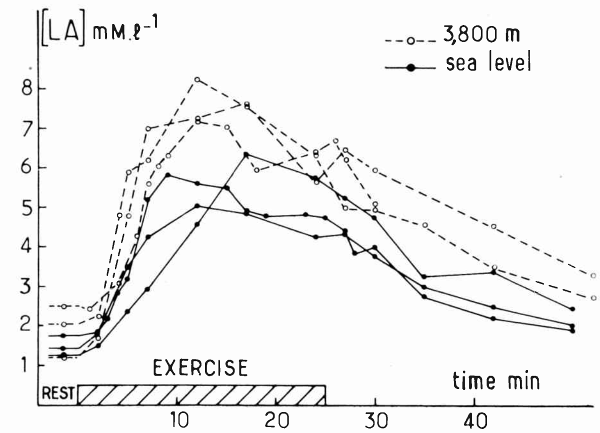

FIG. 8. Lactic acid concentration in brachial venous plasma as a function of time during exercise and recovery in three subjects at SL and HA. Lactic acid determinations were made for highest work load only, corresponding to 90% of $\dot{V}O_{2\ max}$.

total debt at HA is always smaller than at SL. The 1st min debt, which is assumed to represent the largest part of the fast component, increases linearly with the relative work load. The slope and intercept are very near those of deficit (equation for dashed line on Fig. 6). There is no significant difference in the slopes made with the data of 10- or 25-min exercises, so all the points were dealt with collectively. The actual values of the 1st min debt have also been plotted against $\dot{V}O_{2\ st\text{-}st\ ex}$; the slope which has meaning of time is identical in the two environments (0.60 min) and is slightly higher than that of the 1st min deficit (Fig. 4). These results show that the 1st min debt is independent of the duration of exercise and the environment and is linearly connected to energy expenditure exactly as is the 1st min deficit. Figure 8 shows that [LA] is higher at HA than at SL for the same mechanical power but an increased relative work load. The time course of [LA] is similar at SL and HA. However, results which are not reported here show that LA disappears from the blood more quickly at HA.

DISCUSSION

The increase in resting $\dot{V}O_2$ reported here is of the same order of magnitude as found previously in the same subjects when they were studied daily as a function of acclimatization during a sojourn in La Paz the previous year (31). For 7–8 days following arrival, rest $\dot{V}O_2$ oscillates above SL value. Then a significant decrease in $\dot{V}O_2$ and HR of 10% below SL values occurs on the 10th or 11th day of acclimatization. This is probably related to hormonal disturbance. A diminution of urinary excretion of 11-hydroxy- and 17-ketosteroids has been noted on the 8th day of a stay at 2,300 m (27). Afterward, rest $\dot{V}O_2$ increases by about 12% and remains at a higher value than at SL for at least 35 days, during which time the study was made. The present experiments were performed after 3 wk of acclimatization and are situated in the period of increased $\dot{V}O_2$.

Oxygen uptake at steady state of exercise shows no difference at HA and SL in spite of a larger increase in HR and ventilatory rate at HA; cardiac and ventilatory expenditure even during exercise remains very small (16) compared to total energy production, and a possible increase at HA could not be shown because of the lack of sensitivity of the O_2 measurement method. It can be seen on Fig. 1 that gross efficiency is independent of physical fitness, i.e., individual $\dot{V}O_{2\ max}$, and is unaffected by altitude. Similar results have already been reported (1).

Maximal O_2 uptake was indirectly assessed at SL as well as at HA. Even at SL accurate measurement of $\dot{V}O_{2\ max}$ is burdened by a number of practical difficulties. Moreover at HA exhausting exercises are often interrupted by coughing in newcomers. The linear relationship HR versus $\dot{V}O_{2\ st\text{-}st\ ex}$ in Fig. 2 accounts for the use of the indirect method, the most critical point of this technique being HR_{max} determination. However, the data reported by Asmussen (2) show that HR_{max} and age are closely related ($r = 0.97$) over a wide range. In the present study a plus or minus 10 beats·min^{-1} difference in HR_{max} would only induce $\pm$ 8% change in theoretical $\dot{V}O_{2\ max}$. This would not alter the general conclusion. The decrease of 15% in $\dot{V}O_{2\ max}$ at HA agrees with findings of other authors (3, 10, 11, 19, 33). When total deficit and debt at SL and HA are plotted against individual $\dot{V}O_{2\ st\text{-}st\ ex}$, the points are very scattered. The relationship becomes closer when relative work load is used instead of $\dot{V}O_{2\ st\text{-}st\ ex}$. This way of expressing aerobic energy production allows comparison either of different subjects in various states of physical fitness in a given environment or of the same subjects studied in two different environments with physical fitness reduced precisely by the environmental conditions.

Oxygen deficit calculated classically is always larger at HA than at SL. The main effect of HA is to reduce the Po_2 gradient from air to the tissues. Oxygen conductance would have to increase at HA in order to deliver the same amount of O_2 to the working muscles as at SL. However the necessary improvement in conductance is not attained and O_2 transport is impaired in its time course and reduced in its maximal value: O_2 deficit increases and $\dot{V}O_{2\ max}$ decreases.

These last values are related in such a manner that deficit remains connected to relative work load by the same relationship at SL and HA. However, the present study does not deal with the mechanisms involved in this relationship.

Oxygen debt was calculated by subtracting rest $\dot{V}O_2$ from sequent $\dot{V}O_2$ during recovery. Rest $\dot{V}O_2$ seems a better reference for determination of O_2 debt than the "asymptotic" value reached during recovery; the rest value is unquestionable. The term "asymptotic" demonstrates that debt is not over and consequently a part of the studied phenomenon is disregarded. According to these determinations, debt as a whole is always larger than deficit (cf. Fig. 3 and Figs. 6 and 7). However, conditions such as work intensity, duration and environment modify the discrepancy.

It was arbitrarily assumed that the lack or the excess of aerobic energy represented by the 1st min of deficit or debt was mainly related to the splitting or the restorage of the fast creditors. This assumption is an experimental simplification which allowed examination of the components of deficit and debt at HA where fast analyzers were not available and consequently $\dot{V}O_2$ change cycle by cycle could not be described. The step of 1 min was chosen in the light of conclusions given by authors who had studied the initial and final transient phases of muscular exercise. It was reported (25, 26) that $\dot{V}O_2$ varies at first according to an exponential function with a half-time of about 30 s at onset and slightly longer at offset of exercise. Study of the time course of muscular creatine phosphate concentration in dog and man, which brings more direct evidence of the nature and role of the fast component, shows that split creatine phosphate is proportional to load and complete splitting and replenishment are accomplished within 2 min for a given work load (15, 26). So 1st min deficit and 1st min debt seem to be a reasonable index of the fast components. Additionally, it is assumed here that anaerobic glycolysis comes into play late and its role is insignificant during the 1st min of work (28). Keeping in mind these limitations, the slopes of Fig. 4 can be interpreted as time constants of the fast processes of exponential character. Errors necessarily enter into their determination because $d(\dot{V}O_{2\ \text{st-st ex}} - \dot{V}O_{2\ \text{actual ex}})/dt$ is integrated during 1 min instead of infinitely. In spite of these inaccuracies, the so-called deficit time constant (0.54 min) is identical at SL and HA; it is consistent with data previously reported. As Lohman's reaction is independent of P_{O_2}, it was to be expected that the deficit fast component kinetics be unchanged at HA; this hypothesis was verified experimentally. Such a result was already suggested by Cerretelli (7).

The time constant of the fast component of debt is slightly longer than that of the deficit (0.60 min); it is the same at SL and HA. These results would demonstrate that the relative part played by creatine phosphate remains unchanged when the subject is translocated to HA. The replenishment of the stores is affected neither by altitude nor by duration of exercise since slopes calculated with data from 10- and 25-min exercises are not different.

The slow component of the deficit theoretically estimates the energy released by anaerobic glycolysis. In the present experiments, blood [LA], measured at the highest work load only, reaches a larger maximal value at HA than at SL. The intercept of the slope of Fig. 5 would correspond to the anaerobic threshold which appears at about 45 % of $\dot{V}O_{2\ max}$ at SL as well as at HA. The relationship exhibited by Fig. 5 is linear. Hermansen and Saltin (14) also report that when blood [LA] is related to relative work load, all values from different acute altitude fall on the same line.

The interpretation of the slow component of the debt is more questionable. There was no attempt to find two or three slow components in extra $\dot{V}O_2$ during recovery since fitting more than one exponential curve to scattered experimental data is unreliable. Therefore after subtracting the fast component, independent of duration and environment as seen above, from the total debt, the whole remaining extra $\dot{V}O_2$ volume was considered as a single slow component. Classically, a part of extra $\dot{V}O_2$ during recovery is supposed to oxidize LA. However, Fig. 8 shows that [LA] attains peak value around the 10th min of exercise and then decreases during steady-state exercise. The disappearance rate is not affected by the stop of exercise; it would therefore be risky to attribute the slow component of the debt entirely to LA metabolism, all the more because a higher [LA] occurs at HA simultaneously with a smaller debt slow component (Figs. 7 and 8). A similar finding was observed by Reynafarje and Velasquez (32). Consolazio et al. (8) have reported too that a significant decline in O_2 debt occurred at HA. This challenging result has given rise to another series of experiments at HA (34). It was shown that in subjects translocated to HA the body shell cools off during exercise and for about 30 min of recovery due to decreased cutaneous blood flow and greater evaporative rate. On the contrary, at SL the shell warms up during exercise and skin temperature returns slowly to rest value during recovery. Thus one-fifth of body mass is not in the same thermal conditions at HA as at SL. These results argue in favor of a role of temperature in the long lasting increased $\dot{V}O_2$ after exercise. Cain (6) recently pointed out the interaction of temperature with other more specific factors related to exercise and environment on O_2 consumption during exercise. On the other hand, Brooks et al. (5) have emphasized the striking effect of temperature on mitochondrial functions. However, the results reported here do not allow quantification of the contribution of the temperature factor to the magnitude of O_2 debt.

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