

Energy balance during moderate exercise at altitude

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VARENE, P., C. JACQUEMIN, J. DURAND, AND J. RAYNAUD. *Energy balance during moderate exercise at altitude.* J. Appl. Physiol. 34(5): 633–638. 1973.—The purpose of this study was to determine the effects of chronic hypoxia on heat exchange mechanisms during exercise in acclimatized and unacclimatized subjects at altitude. Core temperature increased by the same increment at the end of exercise in all subjects, whereas mean skin temperature rose in subjects in their own environment and decreased in unacclimatized subjects. The energy balance was calculated by partitioned calorimetry. The body stored heat during entire exercise in each case; radiant plus convective heat loss rate was lower and evaporative loss rate higher for lowlanders when relocated at altitude than at sea level. Thermoregulatory mechanisms were unaffected at altitude by either relative work load or barometric pressure. However, the relative part played by heat-dissipating mechanisms was different.

partitioned calorimetry at altitude; body temperature; temperature regulation; acclimatization

KINETICS OF O_2 UPTAKE and lactic acid production during exercise have been studied comparatively, many times at sea level (SL) and high altitude (HA) in lowlanders during acclimatization (6, 8, 15) and in highlanders (11, 18).

Since these data explore total energy production only, it would be interesting to compare the rate of metabolic energy production at SL and HA to the total rate of energy output for the two following reasons: *a*) cutaneous circulation, which is the main component of physiological conductance, decreases at HA (13), and *b*) the time course of O_2 uptake ($\dot{V}O_2$) at onset of exercise and during recovery is different in the same subjects studied at SL and after a sojourn of 3 weeks at HA. Previous studies in subjects during acclimatization have shown the energy production from anaerobic sources at onset of exercise to be greater at HA than at SL (16, 17). The excess $\dot{V}O_2$ above resting level during recovery, classically considered as the payment for the initial O_2 deficit, was also found to be smaller in subjects located at HA than in the same subjects during exercise of identical work load and duration at SL. As it is generally accepted that anaerobic metabolism is less efficient than aerobic (1), calculations of heat exchange by partitioned calorimetry were designed to determine the effects of changes in both skin blood flow and $\dot{V}O_2$ kinetics, induced by HA, on heat exchange mechanisms during

moderate exercise in short acclimatization and in longer acclimatization.

METHODS

The experiments were performed on three lowlanders in Paris (50 m; P_B : 761 torr) and after 3 weeks in La Paz (3,800 m; P_B : 494 torr) and on five highlanders at HA. Lowlanders were physicians 40–44 years old; each subject was tested twice at two locations. Highlanders were soldiers 21–25 years old, exercising once only. The two groups were not comparable precisely, but submaximal work load was expressed in watts per square meter in all the cases. The conclusions drawn from results in the unacclimatized subjects are unquestionable because they were studied comparatively at sea level and at altitude.

Globe (T_g), dry bulb (T_{db}), and wet bulb (T_{wb}) thermocouples, placed near the subjects, were recorded every 10 min. An identical bicycle ergometer was used both at SL and HA.

P_{dp} which is the saturated vapor pressure at dew point temperature (T_{dp}) was calculated from T_{db} and T_{wb} (3):

$$P_{dp} = P_{wb} - [0.5 P_B(T_{db} - T_{wb})/755] \quad (1)$$

where P_{wb} is the saturated vapor pressure at wet bulb temperature (T_{wb}) found by aspiration, and P_B the barometric pressure, in torr.

The esophageal (T_{es}) and rectal (T_{re}) temperatures were recorded by thermocouples inserted 60 cm from the nose and 25 cm from the anus, respectively; 10 skin thermocouples were placed so that the junctions were in contact with the skin. The subjects were dressed in shorts and shoes. An indwelling catheter was positioned in a brachial vein. During rest and recovery periods the subjects sat quietly on a special comfortable chair which replaced the removable bicycle seat. After 1 hr of rest, control measurements and samplings were taken; the subjects were weighed on a scale accurate to ± 10 g (Testut model 294). Submaximal exercise began abruptly and continued for 25 min on a bicycle ergometer (Minjhart type) at constant speed of 60 rpm: the positive work performed (W) was about $53 \text{ W} \cdot \text{m}^{-2}$.

Calibrated copper-constantan thermocouples were connected to a recording potentiometer. The various body temperatures were measured every 2 min. Mean skin temperature (\bar{T}_s) was computed from the average of 10 skin

temperatures weighted in proportion to the size of the site explored (9). The subjects breathed through a mouthpiece: the expiratory valve was connected to a device with two stopcocks for collection of gases in Douglas bags every minute during exercise and the first 5 min of recovery and at longer intervals afterward. Expired gases were analyzed for percent O₂ and CO₂ (paramagnetic and infrared analyzers). The volume of the expired gas collected in a Douglas bag was measured in a Tissot apparatus and the mean minute volume (\bar{V}_E) was calculated accounting for the volume taken off by the analyzers. \dot{V}_{O_2} was computed according to the open circuit method. The ECG was continuously recorded. Blood samples for lactic acid [LA] were drawn at different intervals of time as illustrated by Fig. 3. The subject was reweighed after 5 min of recovery so that the fast component of O₂ debt could be measured during early recovery.

The variables used in the total energy balance equation were at steady state:

$$M = R + C + E + W + S, \text{ in } W \cdot m^{-2} \quad (2)$$

in which M is the rate of aerobic energy production computed from \dot{V}_{O_2} , expressed per unit DuBois area in square meters. Energetic equivalents of 20.27 kJ/O₂ liter at rest and 21.11 kJ/liter at exercise were used in these conversions; the respective respiratory quotient were 0.85 and 1. $R + C$ is the sum of rates of radiant and convective heat loss. E is the rate of evaporative heat loss. S is the rate of heat storage (positive for body heating; negative for cooling); $R + C$ was calculated with the following linear coefficients (h).

$$h_r = 6.4 \times 0.70 W \cdot m^{-2} \cdot ^\circ C^{-1} \quad (3)$$

The ratio of the body's radiating area to total area was 0.70 (4)

$$h_c = [2.2 + (7.45 \times v^{0.67})] \times (P_B/760)^{0.67} W \cdot m^{-2} \cdot ^\circ C^{-1} \quad (4)$$

where v is wind velocity (in cm·sec⁻¹).

$$h = h_r + h_c \text{ at SL} = 6.6 W \cdot m^{-2} \cdot ^\circ C^{-1} \quad (5)$$

$$h = h_r + h_c \text{ at HA} = 6.1 W \cdot m^{-2} \cdot ^\circ C^{-1} \quad (6)$$

$$R + C = h \times (\bar{T}_{s(t_1, t_2)} - T_g) W \cdot m^{-2} \quad (7)$$

E was calculated from the rate of total weight loss, corrected for expired carbon.

The latent heat of evaporation was 2.4 kJ·g⁻¹. S during every 2 min was calculated as follows (5):

$$S = \frac{\text{body wt (kg)} \times 3.511 \times (0.8\Delta T_{\text{core}} + 0.2\Delta \bar{T}_s)}{A_D m^2 \times 120 s} W \cdot m^{-2} \quad (8)$$

3.155 is the body specific heat (in J·kg⁻¹·°C⁻¹) and W is work rate.

Physiological skin conductance (h_s) was directly and indirectly computed at the steady-state exercise according to the following equations:

$$\text{direct } h_s = (E + R + C)/(\bar{T}_{es} - \bar{T}_s) W \cdot m^{-2} \cdot ^\circ C^{-1} \quad (9)$$

$$\text{indirect } h_s = [M - (W + S)]/(\bar{T}_{es} - \bar{T}_s) \quad (10)$$

RESULTS AND DISCUSSION

Numerical data in the text are given as means ± 1 SD; P indicates the level of statistical significance.

Respiratory Data

Figure 1 gives the mean of the respiratory data as a function of time.

Mean expiratory ventilatory flow (\bar{V}_E STPD L·m⁻²). \bar{V}_E at steady state of exercise is lower in highlanders (3.97 \pm 1.0 liters·m⁻²) and lowlanders at HA (3.90 \pm 0.7) than at SL (4.90 \pm 0.6). The true O₂ changes in the opposite way. A higher extraction coefficient of O₂ (0.26 and 0.19, respectively) confirms the greater efficiency of the ventilatory system at HA (0.17 at SL; $P < 0.001$). These results agree with those of Lefrançois et al. (12).

Aerobic metabolic rate (M) and heart rate. At rest, M is higher for lowlanders translocated to HA (SL: 45 \pm 3.9 W·m⁻²; HA: 54 \pm 4.0; $P < 0.01$). This fact was already described for the same subjects during a previous sojourn in La Paz and confirms the same observation made by other investigators. However, gross M at steady-state exercise is identical for lowlanders at SL and HA (265 \pm 5.0 W·m⁻²; 276 \pm 6.4; not significantly different). M in highlanders is larger (322 \pm 4.0) than in lowlanders because W is slightly higher. However, this discrepancy does not affect the general conclusions. Heart rate at rest (88 min⁻¹) and at steady-state exercise (141 \pm 2) is higher for lowlanders at HA but of the same order of magnitude in the subjects in their own environment (lowlanders at SL: 71 \pm 2; 130 \pm 2; highlanders: 67 \pm 2; 132 \pm 2).

Initial O₂ deficit (DO_2) and final O₂ debt (ΔO_2). DO_2 is the sum of the minute-to-minute difference between \dot{V}_{O_2} at steady state and the sequent value of \dot{V}_{O_2} during transient phase. DO_2 is larger for lowlanders at HA (20.1 \pm 3.6 kJ·m⁻²) than at SL (15.2 \pm 1.9 kJ·m⁻²) and almost identical for the two groups at HA. The [LA] concentration in venous blood which refers to anaerobic metabolism is also higher in lowlanders at HA (SL: 6 \pm 0.3 mM; HA: 7.3 \pm 0.8; $P < 0.05$), but the difference is small. The most evident change lies in ΔO_2 ; ΔO_2 is the sum of the minute to minute difference between recovery \dot{V}_{O_2} and rest \dot{V}_{O_2} . The fast component of the debt, which can be roughly represented by the debt during the first minute of recovery, is identical at SL and HA (17). The oxygen debt is smaller (22.1 \pm 5.0 kJ·m⁻²) due to its slow component in subjects relocated to HA than at SL (27.5 \pm 5.1). Analogous results have already been described but not satisfactorily explained (16, 17). According to the thermal data reported on Fig. 2, the smaller slow component of the debt in unacclimatized subjects at HA is accompanied by lower \bar{T}_s than at SL. Before it can be claimed that causal relationship exists between these two factors more information on muscular metabolism is necessary.

Thermal Data

Environmental data. T_g which represents operative temperature is the same at SL and HA (20.5° C; 20.9° C). Even

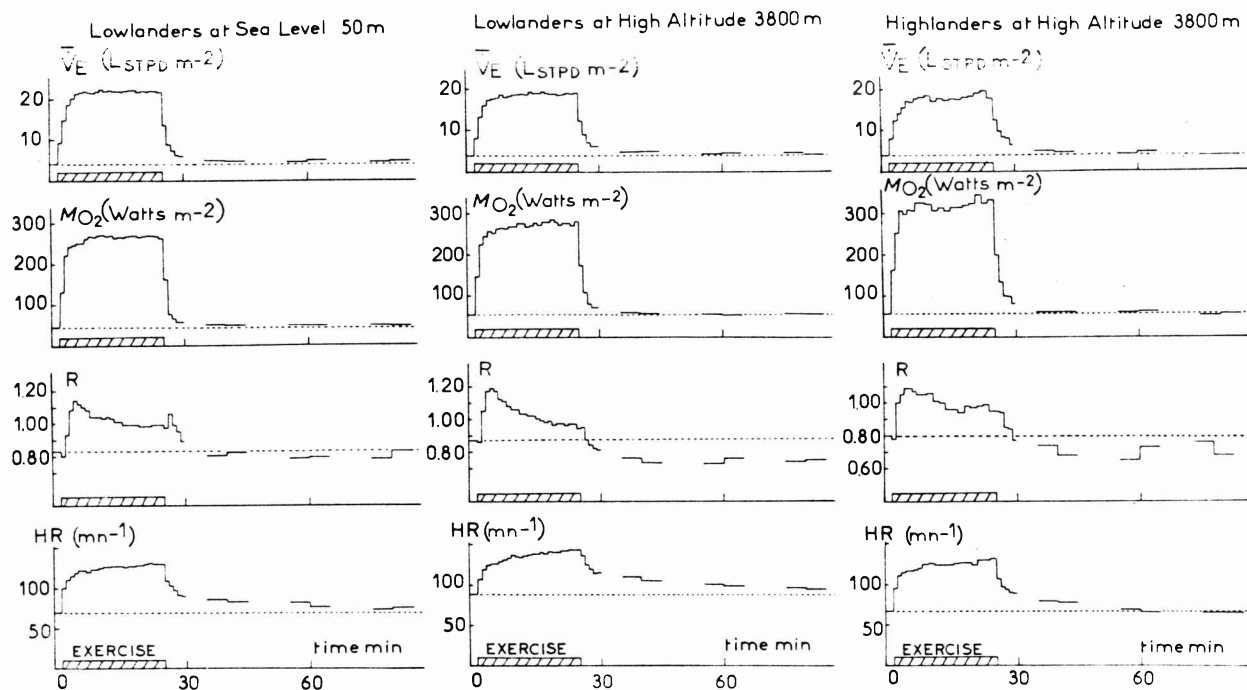


FIG. 1. Mean respiratory data in the three experimental situations as a function of time. Striped area indicates duration of exercise. \dot{V}_E is the mean expiratory flow expressed per square meter. \dot{M}_{O_2} is the aerobic metabolic rate calculated from O_2 uptake, expressed in $W \cdot m^{-2}$. R is the respiratory quotient determined from expired gases. HR is heart rate.

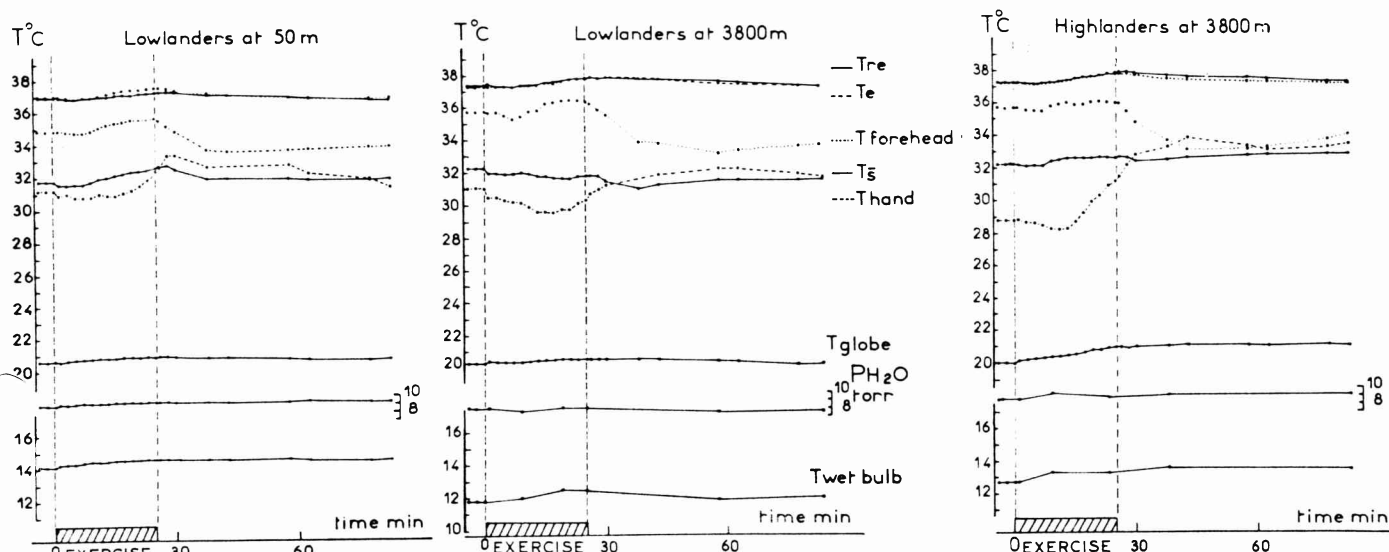


FIG. 2. Mean body temperatures and environmental data as a function of time for three groups of experiments. Forehead T and hand T are given as examples of local T.

though T_{wb} is lower at HA the P_{dp} at dew point temperature is practically the same at SL and HA (eq 1: SL: 9.3 torr; HA: 8.1).

Core and skin temperatures. The increase of T_{re} falls behind that of T_{es} , and at the 25th min of exercise, there is no identity between the two temperatures. The absolute difference of T_{es} between rest and the end of exercise is similar for the three types of experiments (lowlanders at SL: $+0.55^\circ C$; at HA: $+0.57$; HL: $+0.65$; not significantly different).

The T_{re} values are more scattered so calculations including T_{core} are calculated with T_{es} only. In previous simulated

diving experiments (10) using an esophageal catheter in which thermocouples were attached every 5 cm, T_{es} was studied as a function of anatomic references. The thermocouples located near the left atrium and the stomach area gave the same temperature independent of \dot{V}_E .

No plateau was observed in T_{es} : there was a steady temperature increase at the end of exercise.

The most interesting results are: 1) increase of \bar{T}_s at the end of exercise in lowlanders ($+0.85^\circ C$) and highlanders of ($+0.41^\circ C$) in their own environments; and 2) decrease of \bar{T}_s in lowlanders translocated to HA ($-0.47^\circ C$; $P < 0.05$).

Energy Balance Data

a) $R + C$ during rest at SL and HA is larger than M in the three experimental situations. This probably means that the body cools off because the nude surface of the body exposed to air is too large. During this unsteady period, it is difficult to measure a change in T_{es} and T_s . The heat loss by perspiration has not been taken into account. At HA, for a given difference ($T_s - T_a$), C is lower on account of the decreased heat transfer coefficient (h_c).

Besides T_s at the end of exercise in sojourners during acclimatization being cooler than at SL, $R + C$ is diminished (SL: $76 \pm 1.1 \text{ W} \cdot \text{m}^{-2}$; HA: 68 ± 1.0 ; $P < 0.01$).

b) E is calculated from the weight loss measured at the 5th min of recovery. E is not corrected for the respired vapor loss. The chamber valve through which the subject expired and inspired was saturated with water vapor, and it would have been impossible to calculate this loss accurately. Since the present protocol did not allow measurement of weight loss as a function of time, weight loss rate was assumed to be constant throughout the exercise (19).

E is higher in lowlanders at HA ($129 \pm 21.5 \text{ W} \cdot \text{m}^{-2}$) than at SL ($96 \pm 8.1 \text{ W} \cdot \text{m}^{-2}$; $P < 0.05$) and is of the same order of magnitude in highlanders ($127 \pm 10.7 \text{ W} \cdot \text{m}^{-2}$). The increase of E at HA in lowlanders is probably due to a greater sweating rate: in any case sweat does not drip so it is assumed that all the sweat produced was evaporated, and sweating rate is directly correlated to weight loss rate.

c) S was calculated with the same core-shell ratio to body mass at SL and HA (0.8; 0.2). The decrease of T_s is responsible for the smaller S in lowlanders at HA ($47 \pm 8.7 \text{ W} \cdot \text{m}^{-2}$) than at SL (57 ± 4.5); S in highlanders (58 ± 9.1) is slightly higher than in sojourners because T_s does not decrease in these subjects. However, the differences are not statistically significant.

Figure 3 shows the time course of energy balance calculated every 2 min for the three experimental situations. This figure compares aerobic energy input rate to the sum of the energy output rate. Moreover, according to several hypotheses [LA] would allow an estimation of anaerobic metabolic rate at the beginning of muscular exercise. However, the study of the transient phases of energy production as well as of energy output involves too many hypotheses about core-shell ratio and E for them to be discussed conclusively. It can be said from Fig. 3 that energy output exhibits a different time course in unacclimatized subjects at HA compared to SL, but it is impossible to relate metabolic events to caloric events or inversely in the present experiments.

So balance at steady state only has been taken into account in the discussion. It was calculated from the mean values obtained during the last 10 min of exercise.

Every element of the balance is calculated independently from the other. There is good experimental agreement (Fig. 4.4) between the two members of the theoretical equation 2. Since M was not exactly identical in lowlanders and highlanders energy output rates are reported in percentage of total value in Fig. 4B. Therefore, it is easier to compare the different heat loss mechanisms in the three experimental situations. The results show that at metabolic steady state, E represents 34% of total heat loss rate in lowlanders at SL and 44% at HA; E substantially increases

in lowlanders at HA and is higher than in highlanders (40%).

Figure 4B demonstrates that the relative part played by the different mechanisms involved in heat loss is roughly identical in subjects in their own environment.

Physiological conductance was calculated by two independent methods: direct method using equation 9 and indirect method using equation 10. Since Fig. 4A depicts a rather good equality between the two terms of the balance, it is not surprising to find a very small difference between the values of h_s computed by the two methods. Only h_s directly calculated is reported: h_s in lowlanders at HA ($33 \pm 3.7 \text{ W} \cdot \text{m}^{-2} \cdot ^\circ\text{C}^{-1}$) is slightly lower than at SL (37 ± 2.4), however not significantly, though h_s of every subject is lower at HA; h_s in highlanders is $40 \pm 5 \text{ W} \cdot \text{m}^{-2} \cdot ^\circ\text{C}^{-1}$, not different from lowlanders at SL.

General Discussion

Four results must be emphasized. First, as shown on Fig. 2 the body stores heat continuously. Thermal steady state is

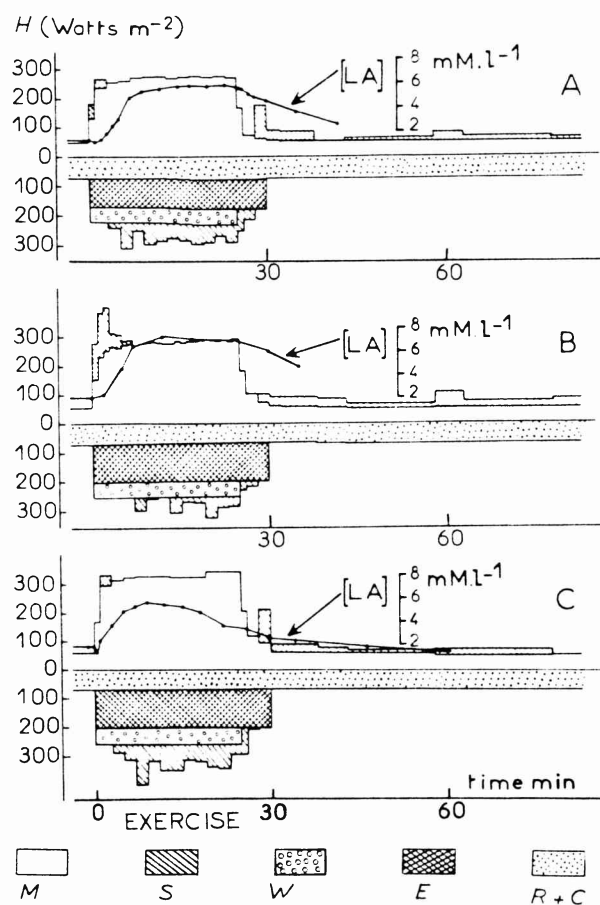


FIG. 3. Energy rate (H) expressed in $\text{W} \cdot \text{m}^{-2}$ as a function of time. Above 0 line, total energy production is reported: aerobic metabolic rate (M) and negative heat storage rate (S). Time course of the venous lactic acid concentration is superimposed. According to numerous hypotheses, it would be possible to calculate anaerobic metabolic rate at the beginning of exercise. Below 0 line, total energy output rate is reported: $R + C + E + S + W$. Mechanical power (W) is constant during exercise. Evaporative heat loss rate (E) is considered as constant. The rate of radiant and convective heat loss ($R + C$) and rate of (S) are calculated for 2-min periods. A: lowlanders at 50 m; B: lowlanders at 3,800 m; C: highlanders at 3,800 m.

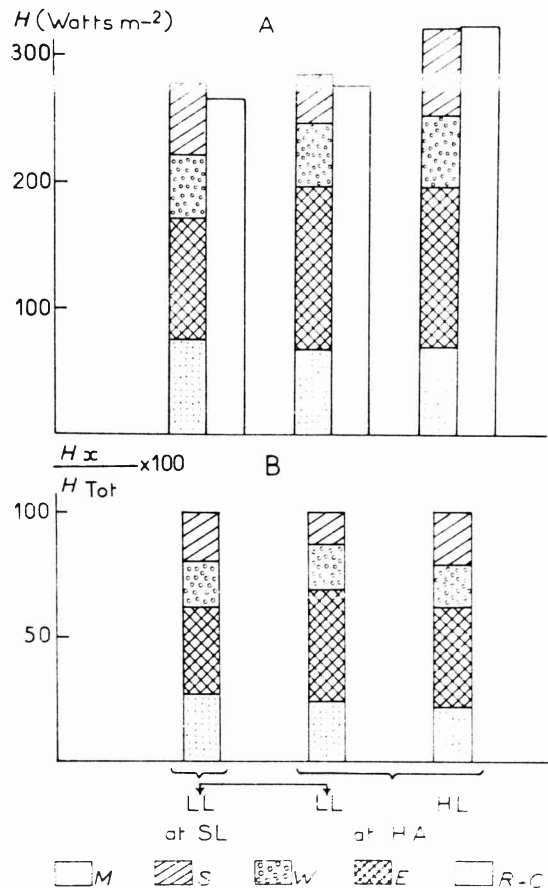


FIG. 4. A: energy balance in absolute values according to the equation: M at steady state = $R + C + E + W + S$; M = aerobic metabolic rate; $R + C$ = sum of rates of radiant and convective heat loss; E = rate of evaporative heat loss; W = work rate; S = rate of heat storage. Balance is computed from the mean of the data obtained during steady state O_2 uptake (from the 15th to 25th min of exercise). B: different energy output rates (H_x) expressed in relative values. Sum ($R + C + E + W + S$) in A, that is total energy output rate H_{Tot} , is taken as equal to 100%.

reached neither at the 25th min of exercise nor later, as previously reported (20). Second, M is identical in the three experimental situations. Hence, if the efficiency is assumed identical at SL and HA the absolute heat load is comparable at SL and HA. Third, the rise in T_{re} is the same for subjects at HA and SL; so the results of the thermoregulatory response are affected neither by the decrease of P_b nor by the relative work load which increases at HA because of the decrease of $\dot{V}\text{O}_{2\text{max}}$. These results agree with Asmussen and Nielsen (2) and Greenleaf et al. (7) and support the hypotheses of Nielsen and Nielsen (14) that the

level of core temperature is not affected by environmental conditions and depends on thermoregulatory adjustments only. Fourth, Fig. 4.1 shows that experimental energy data closely fit the theoretical equation of energy balance. Hence, it seems justified to calculate energy balance during exercise using the same core-shell ratio in the calculation of S as at rest.

High altitude acts on the responses of organism in two ways: one, physical, related to decrease of P_b ; the other, physiological, related to reduced O_2 delivery to the tissues produced by hypoxia. This latter effect is especially remarkable when O_2 demand is increased at exercise. The decrease of P_b induces a change in h_c (eq 4), so that C is necessarily decreased at HA for identical T_g . Evaporative ability of environment is greater at HA than at SL for the same ambient T_{dp} and T_g because the mean free path of the gaseous water molecules is increased when P_b is low.

During exercise the circulatory system has to satisfy two simultaneous needs: 1) an increase in blood flow to working muscles for O_2 and fuel supply, and 2) an increase in blood flow to the skin for heat dissipation.

In this conflicting situation the partition of blood flow is different at SL and HA. At HA there is a relative reduction in cutaneous circulation at rest and exercise (13) probably for the benefit of the working muscles during exercise. The reduction in skin blood flow is partly responsible for cooling the skin: $R + C$ and calculated shell component of S are consequently decreased. The results show that identical increase of core temperature is the final result of thermoregulatory adjustments in response to an identical heat load in the three experimental situations. Since $R + C$ and S decreased in lowlanders translocated to HA, from a theoretical point of view E should be expected to be larger. This logical necessity is verified experimentally.

In model regulator terms (21), HA modifies too the structure of the passive system since cutaneous circulation is decreased. However, the overall response of the active system, at least for moderate exercise, is as effective as at SL.

In conclusion, HA changes the relative part of heat dissipating mechanisms: E becomes higher and T_s cooler. The same heat flow from the core to the shell is possible in spite of a decrease in skin blood flow because the difference of temperature between core and shell is larger. The mechanisms of these new adjustments remain unclear.

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