Anaerobic metabolism during pubertal development at high altitude

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FELLMANN, NICOLE, MARIO BEDU, HILDE SPIELVOGEL, GUY FALGAIRETTE, EMMANUEL VAN PRAAGH, JEAN-FRANÇOIS JARRIGE, AND JEAN COUDERT. Anaerobic metabolism during pubertal development at high altitude. J. Appl. Physiol. 64(4): 1382-1386, 1988.—In a previous study we showed that there were no differences in anaerobic metabolism between groups of 11-yr-old children living at high (3,700 m) and low (330 m) altitudes. The aim of this study is to investigate changes in this metabolism during pubertal development. We compare blood lactate concentration ([L]) after maximal bicycle exercise in 20 boys acclimatized to high altitude (HA, 12 yr old) and at low altitude in 14 boys (LA1, 12 yr old) and in 13 boys (LA2, 14 yr old). The subjects had the same level of physical fitness and the same nutritional and socioeconomic status. Pubertal development was identified by salivary testosterone concentration ([T]). Results (means ± SE) showed 1) at the age of 12 years, [L] and [T] in HA were significantly higher than in LA1 ([L] was 9.2 ± 0.5 vs. 6.8 ± 0.5 mmol/l, [T] was 233 ± 66 vs. 122 ± 30 pmol/l). 2) [L] and [T] in HA were statistically the same as in LA2 ([L] and [T] in LA2, and 3) a linear relationship between [L] and [T] was significant (P < 0.05) in all HA and LA subjects. This suggests that the higher [L] in 12-yr-old boys living at HA could result in an enhanced anaerobic metabolism linked to an earlier gonadal maturation evaluated by testosterone level.

Subjects

With their parents’ consent, three groups of boys were compared; one group [12-yr-old boys (n = 20)] at HA and two groups [one group of 12-yr-old children (n = 14, LA1) and the second group of 14-yr-old subjects (n = 13, LA2)] at LA. The HA boys were either high-altitude natives or had lived for ≥3 yr in La Paz. All the boys were from the French-Bolivian School and had a good nutritional and socioeconomic status. They had the same level of physical fitness (5 h/wk).

Experimental Procedure

At HA environmental parameters (mean ± SD) were 497.2 ± 1.2 Torr for barometric pressure (PB) and 20.3 ± 1.1°C for ambient room temperature (TA). For LA studies PB was 722.3 ± 6.6 Torr and TA was 21.4 ± 1.4°C.

Salivary testosterone level. We chose testosterone concentration in saliva as an objective marker of pubertal development for the ease of saliva collection. The concentration of the steroid was determined by a specific radioimmunoassay for testosterone (15). Saliva (1-3 ml) was extracted with 5 ml of diethyl ether, and the mean recovery rate was >90%. Testosterone antiserum was produced in rabbits immunized with testosterone-11-hemisuccinate-bovine serum albumin. The cross-reactivation values were 100% testosterone, 57% dehydrotestosterone, 1% 3α-androstenediol, and 1% androstenedione.

IN A PREVIOUS STUDY (8) we suggested that chronic exposure to high altitude (HA, 3,700 m, La Paz, Bolivia) did not modify the anaerobic metabolism in 11-yr-old boys. Children who were high-altitude natives exhibited the same blood lactate concentration after a maximal exercise test and the same supramaximal O2 debt and ventilatory threshold as children living at a low altitude (LA, 330 m, Clermont-Ferrand, France). It has been widely accepted that the increase in lactate production throughout the teenage period is linked to pubertal development. Previous investigations found that the ability to form lactate is reduced in young boys up to the age of 10-11 yr (7). Eriksson et al. (6) have found a significant correlation between muscle lactate after maximal exercise and testicular volume in 12-13-yr-old boys. Glycolytic enzyme activities such as aldolase, phosphofructokinase, and lactate dehydrogenase (2, 12) are always lower than in adults. In contrast, activities of oxidative muscle enzymes (lipoamide dehydrogenase and tricarboxylic acid cycle enzymes) are higher than in adolescents and adults. Thereafter, during the pubertal phase, glycolytic capacity increases while oxidative activities decrease slowly but remain significantly higher than in adults. Thus the ratio of pyruvate to lactate-pyruvate oxidized is lower than in adults (12). So far no one has examined the effects of chronic hypoxia on these pubertal changes. The purpose of the present study, therefore, was to compare blood lactate concentration at both altitudes after maximal exercise testing in boys older than those selected for our previous study. Pubertal development was identified by salivary testosterone concentration.

MATERIALS AND METHODS

Subjects

With their parents’ consent, three groups of boys were compared; one group [12-yr-old boys (n = 20)] at HA and two groups [one group of 12-yr-old children (n = 14, LA1) and the second group of 14-yr-old subjects (n = 13, LA2)] at LA. The HA boys were either high-altitude natives or had lived for ≥3 yr in La Paz. All the boys were from the French-Bolivian School and had a good nutritional and socioeconomic status. They had the same level of physical fitness (5 h/wk).

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The intra-assay coefficient of variation was 8.5%.

Blood lactate after maximal exercise. We evaluated [L]m during exercise (Table 1). Salivary testosterone levels at HA were 2 mmol/l (P < 0.005). At HA, VO₂max was significantly higher in 14-yr-old boys than in 12-yr-old boys (P < 0.005). However, there was no difference when VO₂max was corrected for body weight. HRmax and R were the same. [L]max was significantly increased by 2 mmol/l (P < 0.005) in LA₂ group.

The comparison of HA and LA₂ groups showed that VO₂max with and without correction for body weight was reduced by 21% at HA. However, [L]max was statistically the same for the both groups (HA = 9.2 ± 0.5 and LA₂ = 8.7 ± 0.8 mmol/l).

DISCUSSION

The most striking finding to emerge from this study was the higher mean level of blood lactate reached after maximal exercise by HA boys, whereas in our previous study (8) lactate concentrations in 11-yr-old boys were the same at both altitudes.

It is unlikely that these changes at HA were due to methodological differences. Method and materials used for all the studies were the same. We excluded from the study the following exercise bouts for which maximal lactate criteria were not valid: actual exhaustion of boys, above the unit, and failure to further increase the HR. The timing of blood collection (1–2 min after the end of exercise) corresponded to the period during which lactate levels reached their maximal level at both altitudes. A previous study (unpublished data, see Fig. 1) showed that the highest values for HA and LA₂ were at the 2nd and 3rd min and for LA₁ at the 1st min of the recovery period. In each group, values at the 1st, 2nd, and 3rd min were statistically the same.

These findings raise two questions. 1) Would the increase in lactate level at HA be secondary to an increase in muscular production linked to sexual development, and could this early anaerobic maturation be linked to HA environment, and/or 2) could changes in the rate of lactate diffusion from muscle into circulating blood and the rate of lactate utilization by the liver, heart, and muscles at HA explain differences observed in blood lactate concentrations?

From salivary testosterone data (Table 1), boys at HA were indeed in earlier maturation than boys at LA at the same chronological age of 12 yr. The mean salivary testosterone level at HA indicated a pubertal stage no. 3 (300 ± 72 pmol/l, mean ± SD) according to Sannika et al. (26), whereas LA boys exhibited a lower mean salivary

Table 1. Comparisons of anthropometric data and salivary testosterone levels in boys at HA and LA

<table>
<thead>
<tr>
<th></th>
<th>n</th>
<th>Age, yr</th>
<th>Body Mass, kg</th>
<th>Height, cm</th>
<th>Body Surface Area, m²</th>
<th>Salivary Testosterone, pmol/l</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA₁</td>
<td>14</td>
<td>12.38±0.17</td>
<td>43.1±2.0</td>
<td>152.4±2.3</td>
<td>1.36±0.03</td>
<td>132±30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>11.25–13.17</td>
<td>33.8–50.0</td>
<td>138.4–171.5</td>
<td>1.15–1.61</td>
<td>90–173</td>
</tr>
<tr>
<td>P (LA₁ vs. HA)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>&lt;0.001</td>
<td>233±66*</td>
</tr>
<tr>
<td>HA</td>
<td>20</td>
<td>11.98±0.19</td>
<td>37.7±1.3</td>
<td>147.0±2.0</td>
<td>1.25±0.03</td>
<td>244±117</td>
</tr>
<tr>
<td></td>
<td></td>
<td>10.67–13.17</td>
<td>29.0–50.5</td>
<td>134.0–164.5</td>
<td>1.05–1.51</td>
<td>96–401</td>
</tr>
<tr>
<td>LA₂</td>
<td>13</td>
<td>14.24±0.18</td>
<td>51.6±2.4</td>
<td>163.0±1.9</td>
<td>1.54±0.04</td>
<td>167–566</td>
</tr>
<tr>
<td></td>
<td></td>
<td>13.42–15.25</td>
<td>41.0–67.2</td>
<td>154.2–174.9</td>
<td>1.36–1.78</td>
<td>167–566</td>
</tr>
</tbody>
</table>

Values are means ± SE with ranges; n, no. of subjects. When 12-yr-old boys at low altitudes (LA) and high altitudes (HA) (LA₁ vs. HA) were compared, significant values were obtained. When HA boys and 14-yr-old boys at LA (HA vs. LA₂) were compared, LA₂ values were higher than HA values except for salivary testosterone levels, which were the same (*). All values in 14-yr-old boys are higher than in 12-yr-old boys. NS, not significant.
TABLE 2. Comparisons of bioenergetic data for maximal exercise at HA and LA

<table>
<thead>
<tr>
<th></th>
<th>VO₂\text{max}, l STPD/min</th>
<th>VO₂\text{max}, ml STPD-min⁻¹·kg⁻¹</th>
<th>HR\text{max}, beats/min</th>
<th>R</th>
<th>VE, l STPD/min</th>
<th>[L]\text{max}, mmol/l</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA₁</td>
<td>2.01±0.08</td>
<td>47.1±1.5</td>
<td>201±2</td>
<td>1.14±0.06</td>
<td>82.02±3.50</td>
<td>6.8±0.5</td>
</tr>
<tr>
<td>n</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td>P (LA₁ vs. HA)</td>
<td>&lt;0.001</td>
<td>&lt;0.005</td>
<td>&lt;0.001</td>
<td>NS</td>
<td>&lt;0.001</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>HA</td>
<td>1.53±0.08</td>
<td>40.9±1.1</td>
<td>186±2</td>
<td>1.12±0.02</td>
<td>74.35±2.76</td>
<td>8.2±0.5</td>
</tr>
<tr>
<td>n</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>P (HA vs. LA₂)</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>NS</td>
<td>&lt;0.001</td>
<td>NS</td>
</tr>
<tr>
<td>LA₂</td>
<td>2.70±0.18</td>
<td>52.1±1.9</td>
<td>196±2</td>
<td>1.18±0.03</td>
<td>103.44±5.74</td>
<td>8.7±0.8</td>
</tr>
<tr>
<td>n</td>
<td>13</td>
<td>13</td>
<td>13</td>
<td>13</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>P (LA₂ vs. LA₁)</td>
<td>&lt;0.005</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>&lt;0.005</td>
<td>&lt;0.005</td>
</tr>
</tbody>
</table>

Values are means ± SE; n, no. of subjects. Significant values are obtained when 12-yr-old boys at high altitude (HA) and low altitude (LA) (LA₁ vs. HA), 12-yr-old boys at HA and 14-yr-old boys at LA (HA vs. LA₂), and 14-yr-old and 12-yr-old boys at LA (LA₂ vs. LA₁) are compared. VO₂\text{max}, maximal O₂ uptake; HR\text{max}, maximal heart rate; R, respiratory exchange ratio; VE, minute ventilation; [L]\text{max}, maximal lactate concn; NS, not significant.

![FIG. 1. Time course of venous blood lactate concentrations [L] (means ± SE) in 13 boys for each group at high altitude ([HA] 12 yr old (A), and low altitude (LA₁) 12 yr old (O), LA₂, 14 yr old (●)) during a passive recovery after progressive submaximal exercise. Last relative work intensities were same for 3 groups (mean value = 92 ± 6% maximal O₂ uptake). At each time, significant values were obtained when compared: HA vs. LA₁ (* P < 0.05; ** P < 0.01) and LA₂ vs. LA₁ († P < 0.05). HA and LA₂ values were statistically same at any time. Comparisons among rates of [L] disappearance calculated from individual exponential curves using resting [L] level as asymptote revealed a significantly shorter half time in HA (8.8 ± 2.8 min) than in LA₁ (14.4 ± 5.5 min, P < 0.01) and in LA₂ (13.1 ± 6.6 min, P < 0.05).](image)

testosterone concentration corresponding to stage no. 2 (115 ± 31 pmol/l, mean ± SD). Our findings were especially interesting because salivary testosterone is closely related to plasma-free testosterone, which interacts with specific receptors in the target cells and consequently is considered as the physiologically effective steroid (16, 27). In 1973 Eriksson et al. (6) found a significant correlation between muscle lactate after maximal exercise and testicular volume in 12- to 13-yr-old boys. Moreover the direct effect of testosterone on muscle metabolism has been well documented in animals. These studies were made either on “androgen-sensitive” muscles, the temporal muscle of guinea pig (1) and levator ani muscle of the rat (5), or on muscles that are not androgen sensitive, the soleus and gastrocnemius in rats (18). Enzyme patterns in guinea pig muscle changed to male type
during sexual maturation under the effect of androgens. The male temporal muscle showed "a relative predominance of all enzyme activities connected with glycolysis (1)." Castration in rats was accompanied by a decrease in the diameter of the white fibers (5), a decrease in the fast-twitch high-oxidative (type IIa) muscle fibers, and in phosphorilase and lactate dehydrogenase activities in the white muscle (18). No biochemical change was found in red muscle. Testosterone substitution reversed these changes. Furthermore, testosterone injection in young female guinea pigs increased activities of glycolytic enzymes (1).

These observations suggest that boys at HA produce more lactate than boys at LA because they are mature at an earlier age. Two observations seemed to confirm this hypothesis. First, when the 12-yr-old boys at HA and 14-yr-old boys at LA were compared, mean testosterone levels were the same as were blood lactate levels. On the other hand, a significant linear relationship between blood lactate and salivary testosterone was found among all the boys investigated (Fig. 2): the higher the level of blood lactate and salivary testosterone was found among 12 (♂) and 14 (♂) yr.

To conclude, the higher lactate concentration observed at HA than at LA in boys of the same chronological age of 12 yr could result in a higher lactate muscle production linked to an enhanced maturation of anaerobic metabolism.

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REFERENCES


8. FEHLMANN, N., M. REUH, H. SPIELVOGEL, G. FALCAIRETTE, E.