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Anaerobic threshold, muscle volume and hypoxia

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Summary. Ventilatory threshold, apparent mechanical efficiency, oxygen debt repayment, heart rate and perceptions of exertion at the ventilatory threshold have been examined in 8 men and 8 women during the performance of four types of exercise (2-leg, 1-leg, arm plus shoulder, and arm ergometry) under normoxic and hypoxic (12% oxygen) conditions. The ventilatory threshold (percentage of task-specific $\dot{V}_{O_{2peak}}$ at which a disproportionate increase of ventilation begins) was not significantly affected by the sex of the subject, by hypoxia, or by the volume of active muscle involved in the activity, but showed poor reproducibility in small muscle tasks. The apparent mechanical efficiency in 2-leg ergometry was increased from 25.7 to 28.1% under hypoxic conditions, presumably reflecting an increased contribution of anaerobic effort to sub-maximal work. However, oxygen debt repayment following exhausting exercise was much smaller for arm than for leg ergometry. The heart rate corresponding to the ventilatory threshold decreased as the volume of active muscle was reduced. General and respiratory perceptions of effort were rather light for self regulation of an exercise prescription to the ventilatory threshold, and particularly with tasks involving the arm muscles, prescription may best be regulated by the intensity of local muscular sensations.

Key words: Anaerobic threshold — Ventilatory threshold — Oxygen debt — Muscle volume — Hypoxia

Introduction

The concepts of ventilatory and lactate thresholds (Hollmann 1961; Wasserman and McIlroy 1964) remain somewhat controversial (Davis 1985; Brooks 1985). Nevertheless, the present authors can envisage a situation where the rate of diffusion of hydrogen ions and/or lactate from working muscles with an inadequate oxygen supply exceeds the combined clearance capacity of non-exercising muscle, liver, kidneys and heart, leading to a sharp decrease of blood pH (Jones 1980; Hetenyi et al. 1983) and the onset of disproportionate hyperventilation; this we define as the ventilatory threshold.

Davis et al. (1976) found a lower threshold for arm cranking than for 2-leg ergometry or treadmill running (47% versus 64% and 59% of $\dot{V}_{O_{2\,max}}$). They suggested that this finding could have arisen because their subjects were habitual cyclists. Their observations were subsequently replicated by Paterson and Morton (1986). Neary and Wenger (1986), on the other hand, found a higher ventilatory threshold with one leg than with two legs (64% vs 52%). Certainly, the rate of hydrogen ion production per unit of tissue is likely to be greater if the volume of muscle involved in a task is sufficiently small that performance is limited by local muscular perfusion rather than by the maximum cardiac output, and fast twitch glycolytic fibres must be recruited in order to develop the requisite forces. However, as the total volume of active muscle is reduced further, the maximal rate of glycolysis will also decrease, making it more likely that a balance will be struck between the production and the circulatory clearance of anaerobic metabolites. If the ventilatory threshold does indeed provide a simple indication of the onset of local muscular hypoxia, it should also oc-

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cur at a lower work-rate as the percentage of inspired oxygen is reduced (at least in tasks where maximum performance is normally determined by circulatory factors).

Theses issues are important if breathlessness is to be used as a guide to the prescription of various types of aerobic exercise, both at sea level and in mountainous regions. We thus undertook experiments to determine ventilatory threshold on four types of ergometer, using graded muscle volumes from 1 to 15 l, under normoxic and hypoxic (12% oxygen) conditions.

Methods

Subjects and experimental plan. The subjects were 8 male and 8 female volunteers drawn from the university community. Physical characteristics are summarized in Table 1. Most of the group were moderately active, but none were highly trained. One of the women used a roadster cycle regularly for moderately-paced transportation in the Paris area.

Table 1. Physical characteristics of subjects (mean ± SD)

	Men	Women
Age (y)	28.6 ±3.8	31.9 ±10.4
Height (m)	1.81* ±0.07	1.63 ±0.04
Body mass (kg)	70.2* ±8.7	54.1 ±4.3
Skinfold thickness (average of 4, mm)	7.1* ±1.7	9.6 ±2.2
Body fat (%)	13.1* ±3.2	24.3 ±3.1
Lean mass (kg)	59.8* ±8.2	38.9 ±5.8
Leg volume		
total (l)	9.86 ±1.8	8.8 ±0.9
muscle (l)	7.68* ±1.3	5.65 ±0.6
fat (l)	1.17* ±0.5	2.38 ±0.3
bone (l)	1.10* ±0.2	0.75 ±0.15
Arm volume		
total (l)	2.52* ±0.3	1.74 ±0.2
muscle (l)	1.80* ±0.2	1.08 ±0.1
fat (l)	0.31* ±0.1	0.41 ±0.05
bone (l)	0.41** ±0.1	0.24 ±0.03
Maximum oxygen intake (ml kg^{-1} min^{-1})	49.1 ±7.1	40.9 ±10.3

* $p < 0.05$; ** $p < 0.01$

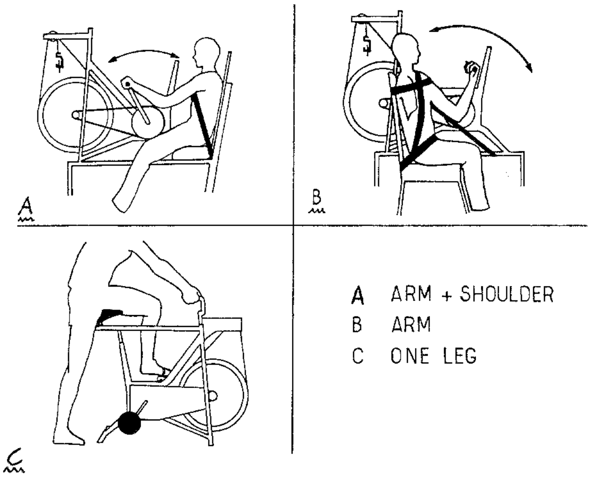

Fig. 1. Diagram illustrating the arrangements of ergometer used in these experiments

After a preliminary medical and anthropometric examination, a habituating test was performed on the cycle ergometer. A further eight ergometer tests were then carried out at intervals of 2–3 days, according to a Latin square design. Four types of ergometer (2-leg, 1-leg, arm plus shoulder and arm) were used under normoxic and hypoxic conditions.

Ergometer protocol. The four ergometers were based on a familiar design (Monark) (Fig. 1). The 2-leg ergometer was modified by fitting a high saddle-pillar, racing saddle, rat-trap pedals, and an induction counter to monitor the metronome-paced pedal rhythm of 50 revolutions·min^{-1}. The 1-leg ergometer was further modified by clamping a 12 kg mass to the right pedal, and fitting a long crossbar. The latter enabled the saddle to be displaced up to 50 cm rearward of the normal saddle post; the subject could then fully extent the active (left) leg while keeping the right foot firmly on the ground immediately behind the right pedal.

The arm plus shoulder ergometer was arranged with a comfortable seat and rigid back support at crankshaft height. The subject sat astride the normal saddle pillar and propelled a free flywheel by a lever which replaced the left pedal. A handle, individually adjusted to shoulder height, was grasped palm downwards, and thrust forwards through an arc of 120°. The metronome-paced rhythm of 40 thrusts·min^{-1} was monitored by an induction counter mounted on the flywheel. For arm ergometry, the subject sat at the same height, but facing rearwards. Three tight harnesses immobilized the hips, the trunk and the shoulders, while the upper part of the left arm was provided with a rigid back support. The axis of the elbow was aligned with the crankshaft, and the handle height on the lever was individually adjusted so that it could be grasped comfortably with the palm facing upwards. The apparatus was operated by flexing the elbow through an arc of 120°; the metronome-paced rhythm was again 40 strokes·min^{-1}.

All tests began with a 3 min warm-up at a comfortable light load gauged by the subject's physique and condition (about 30% of the peak $\dot{V}_{O_2}$ for a given exercise mode). After a further 15 min of seated rest on the ergometer, a ramp function protocol was begun at the same loading as that used for the warm-up. The work-rate was increased in even stages, at one minute intervals, with the intention of exhausting the subject in 9–11 min during normoxia, and 7–9 min during hypoxia.

Metabolic measurements. A metabolic cart (Jaeger Ergo-oxyscreen) was used to collect metabolic data at 30 s intervals. Ventilation was sensed by a heated screen flowmeter, calibrated using a one litre pump, oxygen concentrations were determined by paramagnetic analyser, and carbon dioxide concentrations by infrared detector. Gas analysers were calibrated against chemically analysed cylinder mixtures. During the hypoxia experiments, a mixture of 12% oxygen in nitrogen was inhaled from a 2000 litre bag, commencing immediately after the warm-up exercise.

As suggested by Davis (1985), our primary criterion for detection of the ventilatory threshold was the transition from a decreasing to an increasing ventilatory equivalent for oxygen. Many previous authors have neglected to specify the reproducibility of such data. In the two-leg ergometer experiments, our well-habituated subjects gave a clear-cut breakpoint on this criterion. Test-retest coefficients of variation were equal to 15% in two leg-ergometry and 16% in one-leg ergometry. In the arm exercise, the increments of oxygen consumption were much smaller, and ventilatory thresholds were correspondingly less clear-cut, so that sometimes it was necessary to correlate this information with other indicators of the threshold such as an increasing respiratory gas exchange ratio and a change in the relationship of ventilation to work-rate; nevertheless, test-retest coefficient of variation increased to 26% for arm + shoulder work, while in arm work it was as large as 35%.

Net mechanical efficiency was estimated from a linear plot of oxygen consumption against power output, commencing at the figure observed for seated rest on the ergometer, and stopping 1-2 min short of exhaustion. Each litre of oxygen consumed was assumed equal to an energy usage of 20.9 kJ.

Table 2. Ventilatory threshold for 4 types of exercise under normoxic and hypoxic conditions (mean ± SD, L min^{-1} and percent of task-specific $\dot{V}_{O_{2peak}}$)

Condition	2-leg	1-leg	Arm & shoulder	Arm	All types of exercise
Normoxia					
Men	1.79 ± 0.3	1.27 ± 0.2	0.73 ± 0.2	0.63 ± 0.2	
	52.9%	58.0%	59.0%	62.3%	58.0%
Women	1.22 ± 0.3	0.98 ± 0.2	0.56 ± 0.4	0.41 ± 0.2	
	55.4%	62.4%	60.5%	54.0%	58.1%
Men &	1.51 ± 0.4	1.12 ± 0.3	0.64 ± 0.3	0.52 ± 0.2	
women	54.2%	60.2%	60.0%	57.5%	60.0%
Hypoxia					
Men	1.43 ± 0.4	1.18 ± 0.2	0.57 ± 0.1	0.56 ± 0.1	
	57.6%	59.3%	54.0%	62.2%	58.3%
Women	0.85 ± 0.2	0.92 ± 0.2	0.40 ± 0.1	0.41 ± 0.1	
	56.1%	62.4%	59.2%	53.6%	57.8%
Men &	1.14 ± 0.4	1.05 ± 0.2	0.50 ± 0.1	0.49 ± 0.1	
women	56.9%	60.9%	56.6%	58.2%	58.1%

Significance of differences tested by 3 way analysis of variance

Exercise	Ventilatory threshold (L min^{-1})	Ventilatory threshold (percentage of $\dot{V}_{O_{2peak}}$)
Sex	$p < 0.01$	NS
Inspired Oxygen	$p < 0.01$	NS
Concentration	$p < 0.01$	NS

Oxygen debt repayment was examined over the first 5 min of recovery, totals being calculated relative to the immediate pre-exercise resting figures for a given day.

Other measurements. Limb volumes were estimated from lengths (L), circumferences (C), skinfold readings (S) and fat-corrected intercondylar diameters (D), as described by Shephard et al. (1987). In brief:

Total limb volume $= (\sum C^2) L / 12.56 n$
Fat volume $= (\sum C/n)(\sum S/n^1) L$
Bone volume $= (FD)^2\, 3.14 L$
Muscle volume $=$ Total limb volume $-$ (Fat $+$ Bone volume)

where n is the number of circumferences, n^1 is the number of skinfolds, and F is a geometric factor (0.21 for the arm, 0.235 for the leg).

Skinfold measurements were taken at the sites recommended by the International Biological Programme (Weiner and Lourie 1981), and were used to predict body fat and thus lean mass (Durnin and Womersley 1974). Heart rate was monitored by electrocardiogram, using CM5 leads. Blood pressures were measured by standard sphygmomanometer cuff at 1 min intervals, and ratings of perceived exertion (general, respiratory and muscular) were also taken each minute. Arterialized capillary blood was collected at 1.5 and 2.5 min after exercise, peak lactate levels being determined by the Boehringer enzymatic method.

Perceived exertion was rated using a french-language version of the original Borg (1971) scale. Appraisals were made of general, muscular and respiratory sensations throughout the progressive exercise test.

Results

Ventilatory thresholds

Ventilatory thresholds for the four forms of exercise are summarized in Table 2. A 3 way analysis of variance (exercise × sex × inspired oxygen concentration) revealed no significant effect from the volume of active muscle. Likewise, there were no significant main effects attributable to sex or inspired oxygen concentration.

The woman who was a regular city cyclist did not show a remarkable ventilatory threshold. Indeed, both her absolute threshold for this form of activity (0.89 l min^{-1}) and the percentage of $\dot{V}_{O_{2peak}}$ (44.7%) were below the average for female subjects.

Mechanical efficiency

The mean net mechanical efficiency for 2-leg ergometry while breathing air (Table 3) was a little higher than the commonly accepted average figure of 23% (Shephard 1977). However, there was a substantial decrease of efficiency when work was performed with the arms.

Table 3. Mean mechanical efficiency (% ±SD) of four types of work under normoxic and hypoxic conditions. Significance of differences tested by one way analysis of variance (p_1 = sex difference; p_2 = inspired oxygen difference)

Condition	2-leg	1-leg	Arm & shoulder	Arm
Normoxia				
Men	25.9	20.7	7.9	4.9
	±2.1	±1.5	±1.8	±1.1
Women	25.4	21.0	7.6	4.1
	±2.7	±1.2	±2.1	±1.0
Men & women	25.7	20.9	7.8	4.5
	±2.4	±1.3	±1.9	±1.1
Hypoxia				
Men	27.6 ($p_2 < 0.05$)	20.9	8.6	5.3
	±3.2	±1.0	±1.4	±1.6
Women	28.5 ($p_2 < 0.05$)	20.2	7.1 ($p_1 < 0.05$)	4.2
	±4.0	±2.2	±1.5	±1.1
Men & women	28.1 ($p_2 < 0.05$)	20.6	7.8	4.8
	±3.6	±1.7	±1.6	±1.4

Significance of differences tested by 3 way analysis of variance

Exercise	$p < 0.01$
Sex	NS
Inspired Oxygen Concentration	NS

Hypoxia gave rise to a significant increase of net efficiency in 2-leg exercise ($F = 5.12$, $p < 0.05$), but it had little effect upon efficiency for the other three modes of activity.

Oxygen debt repayment

The magnitude of the oxygen debt repayment following exhausting exercise decreased as the volume of active muscle was reduced (Table 4). Debt repayments for two and one-leg exercise were also significantly smaller in women than in men ($p < 0.01$), although these differences disappeared if figures were expressed per kg of lean mass or per litre of active muscle volume. The absolute magnitude of oxygen debt repayment following two-leg exercise was also less under hypoxic conditions than when breathing air ($F = 5.70$, $p < 0.05$).

These differences were mirrored by blood lactate concentrations which at exhaustion averaged 9.2, 6.4, 4.5 and 3.7 mmol l^{-1} for the four types of work when breathing room air and 7.9, 6.5, 4.7 and 3.5 mmol l^{-1} when breathing 12% oxygen. There were also parallel differences in the magnitude and timing of the peak respiratory gas exchange ratios observed following the various bouts of exercise (Table 4).

Table 4. Repayment of oxygen debt over first 5 minutes of exercise. Mean ± SD of results for 4 forms of exercise under normoxic and hypoxic conditions for oxygen debt (L) peak respiratory exchange ratio and timing of this peak (min)

	2-leg	1-leg	Arm & shoulder	Arm
Normoxia				
Men	4.18±0.5	2.47±0.6	0.92±0.42	0.74±0.3
	1.69±0.2	1.53±0.1	1.19±0.2	1.26±0.2
	2.1 ±0.7	2.0 ±0.5	1.6 ±1.1	1.1 ±0.8
Women	2.88±0.9	1.77±0.3	0.78±0.6	0.66±0.3
	1.52±0.3	1.45±0.2	1.07±0.1	1.06±0.1
	2.3 ±0.8	2.6 ±0.6	1.8 ±1.3	2.1 ±1.3
Men & women	3.53±1.0	2.12±0.6	0.85±0.5	0.70±0.3
	1.60±0.2	1.49±0.1	1.13±0.2	1.14±0.2
	2.2 ±0.7	2.3 ±0.6	1.7 ±1.1	1.6 ±1.7
Hypoxia				
Men	3.39±0.5	2.26±0.7	0.74±0.5	0.61±0.3
	1.6 ±0.2	1.37±0.9	1.28±0.2	1.25±0.2
	1.6 ±0.8	1.5 ±0.8	0.8 ±0.5	0.9 ±0.9
Women	2.12±0.6	1.69±0.5	0.69±0.4	0.7 ±0.3
	1.38±0.1	1.22±0.2	1.10±0.2	1.06±0.1
	1.3 ±0.8	1.5 ±0.9	1.6 ±0.9	1.6 ±1.0
Men & women	2.75±0.9	1.98±0.7	0.72±0.4	0.66±0.3
	1.49±0.2	1.30±0.1	1.19±0.2	1.16±0.2
	1.5 ±0.8	1.5 ±0.9	1.2 ±0.8	1.3 ±0.7

Significance of differences tested by 3 way analysis of variance

	oxygen debt	peak R	timing
Exercise	$p < 0.001$	$p < 0.001$	NS
Sex	$p < 0.001$	$p < 0.001$	NS
Inspired Oxygen Concentration	$p < 0.001$	NS	$p < 0.01$

Ratings of perceived exertion

Ratings of perceived exertion corresponding to the ventilatory threshold were all quite low, but were relatively uniform for the four modes of exercise, both in normoxia and in hypoxia (Table 5). General sensations lay in the range 11-13 units ("fairly light" to "somewhat hard" work). Respiratory sensations followed the same pattern. However, local muscular sensations at the ventilatory threshold reached 13-16 units for normoxic conditions ("somewhat hard" to "hard" and above), while lying between 12 and 15 units for hypoxic conditions.

The corresponding heart rates were about 130 bt $\min^{-1}$ for 2-leg exercise, dropping to 120 bt $\min^{-1}$ in 1-leg exercise, and 110 bt $\min^{-1}$ in arm exercise. Hypoxia led to a marginal increase of heart rate at the ventilatory threshold.

Table 5. Ratings of perceived exertion (mean ± SD) corresponding to ventilatory threshold (general, respiratory and muscular sensations)

	2-leg			1-leg			Arm & shoulder			Arm		
	G	R	M	G	R	M	G	R	M	G	R	M
Normoxia												
Men	11.9	12.5	13.4	11.9	11.3	14.0	12.0	11.0	14.8	11.9	10.9	14.4
	±3.3	±3.2	±2.7	±3.3	±3.3	±2.6	±3.4	±3.2	±3.5	±2.8	±3.0	±1.4
Women	10.9	10.8	12.9	10.6	10.0	12.6	12.3	12.0	14.9	10.8	9.9	13.0
	±1.4	±1.2	±1.1	±2.5	±1.4	±2.3	±3.0	±3.3	±2.7	±2.3	±1.8	±3.7
Men & women	11.4	11.6	13.1	11.3	10.6	13.3	12.1	11.5	14.8	11.3	10.4	13.7
	±2.5	±2.5	±2.0	±2.9	±2.6	±2.4	±3.1	±3.2	±3.0	±2.5	±2.5	±2.8
Hypoxia												
Men	11.8	11.5	12.4	10.8	10.9	13.4	10.6	10.3	12.1	9.1	9.4	12.4
	±2.1	±2.3	±2.2	±0.9	±1.7	±1.8	±3.6	±3.4	±3.3	±1.8	±2.8	±3.4
Women	12.1	11.5	11.9	11.4	12.0	12.9	11.5	11.6	13.4	10.8	10.6	12.6
	±3.0	±1.9	±1.8	±2.1	±1.9	±2.1	±3.0	±2.9	±2.4	±2.5	±2.1	±1.9
Men & women	11.9	11.5	12.1	11.1	11.4	13.1	11.1	10.9	12.8	9.9	10.0	12.5
	±2.5	±2.0	±2.0	±1.6	±1.8	±1.9	±3.2	±3.1	±2.9	±2.3	±2.5	±2.7

Discussion

Effects of protocol

The possible influence of the choice of ramp protocol upon the ventilatory threshold has been vigorously debated. Hughson and Green (1982) found that the use of small steps (8 W) reduced the 2-leg threshold relative to larger steps (65 W). In contrast, Wasserman et al. (1973) saw no difference of threshold between 1 and 4 min stages of 25 W.

Our protocol called for a 2-leg ramp function of about 20 W $\min^{-1}$ for the men and 15 W $\min^{-1}$ for the women, with appropriate downward adjustment of step size as the volume of active muscle was reduced. While our choice of a moderately steep ramp function could have modified absolute ventilatory thresholds, it is unlikely to have invalidated comparisons between the four types of exercise.

During hypoxia, the exercise duration was curtailed by 2–3 min, increasing the relative steepness of the ramp function, and based on the experience of Hughson and Green (1982) this could have caused a small increase in anaerobic threshold.

Effect of muscle volume

In contrast to the earlier findings of Davis et al. (1976), which were validated against *venous* lactates, the present results showed a slight rise of ventilatory threshold (expressed as a percentage of the corresponding $\dot{V}_{O_{2peak}}$) with a change in the volume of active muscle.

We conclude that expressing the ventilatory threshold as a percentage of $\dot{V}_{O_{2peak}}$ allows in large measure for differences in the volume of ac-

Table 6. Peak oxygen intake (mean ± SD) for the several modes of work expressed in absolute units ($l \cdot \min^{-1}$) and per litre of active muscle ($ml \cdot \min^{-1} l^{-1}$)

	2 legs	1 leg	Arm & shoulder	Arm
Normoxia				
Men	3.43	2.20	1.23	1.08
	±0.6	±0.19	±0.19	±0.28
	226	294	702	1010
	±8.0	±58	±86	±239
Women	2.23	1.63	0.85	0.82
	±0.6	±0.4	±0.28	±0.28
	198	283	790	1264
	±10.5	±57	±306	±414
Men & women	2.83	1.92	1.04	0.95
	±0.6	±0.28	±0.24	±0.28
	212	289	746	1137
	±9.3	±57.4	±196	±327
Hypoxia				
Men	2.49	2.0	1.11	0.96
	±0.35	±0.22	±0.18	±0.20
	164	260	614	886
	±21.3	±37.2	±137	±184
Women	1.56	1.50	0.84	0.83
	±0.37	±0.31	±0.22	±0.33
	138	265	766	1277
	±34.8	±66.6	±181	±398
Men & women	2.03	1.75	0.98	0.90
	±0.36	±0.27	±0.20	±0.27
	151	263	690	1082
	±28	±52	±159	±291

tive muscle. On the other hand, peak oxygen consumption per unit of limb muscle was substantially greater for arm than for leg work (Table 6). This could reflect a greater peak of local perfusion per unit volume of tissue when using an upper limb, but the very low power output achieved by the arm is against this explanation. Rather, one must envisage an augmentation of local peak oxygen intake through the use of accessory muscles (respiratory muscles, trunk stabilisers, and even contralateral contractions). Some of these accessory muscles may also reach their anaerobic threshold, but others will not. The lactate production per unit of hypoxic muscle also depends on fibre type, although in the average non-athletic individual there is no reason to suppose a major difference of fibre composition between the arms and the legs (Gollnick et al. 1972).

Brooks (1985) has argued that changes of hepatic perfusion have a substantial impact upon lactate clearance and thus blood lactate concentrations. Because the circulatory demands of arm exercise are less than those for leg work, a reduction of hepatic perfusion would have been less likely when performing the arm task; thus, if this factor were important, it would tend to elevate the arm threshold relative to that for leg work. However, the usual hepatic clearance of lactate (0.1–0.2 g min^{-1}, Shephard 1982) is small relative to the overall production of this metabolite and its clearance by the other routes.

Although the peak blood lactate levels are less for arm work, the end result of the various conflicting factors seems a ventilatory threshold that is relatively independent of the active muscle volume.

Effects of hypoxia

If the ventilatory threshold is indeed an expression of local muscular hypoxia, it should be lowered when the inspiration of hypoxic mixtures reduces the transport of oxygen to the active tissues. However, since the peak $\dot{V}_{O_2}$ is also reduced by hypoxia, it remains possible that the relative threshold (percent of $\dot{V}_{O_{2peak}}$) might show no change.

Cerretelli (1967) argued that acute hypoxia did not interfere with mechanisms of glycolysis. Nevertheless, he noted that lactate started to accumulate at lower work-rates during hypoxia, and he described this as a "lowering of the anaerobic threshold." Others have examined subjects with anaemic hypoxia (Woodson et al. 1978) and carbon monoxide exposure (Vogel and Gleser 1972). Although these last two articles did not focus specifically upon anaerobic threshold, they nevertheless found an increased accumulation of lactate at a given work-rate or oxygen consumption, with no change when data were expressed as a percentage of the experiment-specific $\dot{V}_{O_{2peak}}$.

Our results showed hypoxia as having a much greater impact upon oxygen transport in 2-leg ergometry (where the limiting factor is largely cardiovascular function) than in arm work (where the limitation is almost entirely peripheral) (Table 6). However, in keeping with the work of Vogel and Gleser (1972) and Woodson et al. (1978), the ventilatory threshold was unaffected by hypoxia if expressed as a percentage of the task-specific $\dot{V}_{O_{2peak}}$ (Table 2).

Mechanical efficiency

The relatively high average mechanical efficiency for 2-leg ergometry reflects in part the method of calculation (subtraction of the observed resting oxygen consumption, averaging 0.32 L min^{-1} for men and 0.23 L min^{-1} for women, rather than the theoretical figure of 3.5 ml $\text{kg}^{-1} \cdot \text{min}^{-1}$, 0.25 and 0.19 L min^{-1} for men and women respectively). The other possible factor was the use of rat-trap pedals, which allowed a more effective mechanical coupling between the leg muscles and the machine.

The very low mechanical efficiency during arm work may have three possible explanations. 1) Observation of the subjects suggests substantial muscle activity in stabilising the body despite restraining straps. 2) Attempts are also made to use inappropriate muscle groups as the prime movers become fatigued. 3) Energy is lost in reversing movement of the arm plus lever. The importance of the third factor is supported by the much smaller decrease of net efficiency when the task was performed as a smooth rhythmic movement by a single leg.

If a portion of the total work is performed anaerobically, and no account is taken of oxygen debt repayment, then the apparent mechanical efficiency will rise. This seems the most reasonable explanation of the increase in efficiency (from an average of 25.7 to 28.1%) which was seen when 2-leg ergometry was performed under hypoxic conditions. Hypoxia is most prone to affect those forms of exercise where circulation is the main limiting factor. Hence it is understandable that the effect was observed in 2-leg ergometry, but not in the other forms of exercise where a smaller muscle volume was activated.

Oxygen debt repayment

In keeping with the foregoing discussion, the size of oxygen debt repayment bore a general relationship to the volume of active muscle (Table 4) and a close relationship to the corresponding $\dot{V}_{O_{2peak}}$ (Table 6). The five minute repayment figures for 2-leg ergometry were also in keeping with earlier data for the total repayment of lactate and alactate debts (Shephard 1982).

Lessons for exercise prescription

Several important lessons for exercise prescription may be drawn from this research. Firstly, the relationship between heart rate and $\dot{V}_{O_{2peak}}$ is highly task specific. A 65% $\dot{V}_{O_{2peak}}$ prescription corresponds to a heart rate of some 140 beats/min for 2-leg ergometry, but during arm work the corresponding target would be only 115 beats/min for women and 108 beats/min for men. Secondly, the ventilatory threshold is a quite variable target, particularly if the muscle mass involved in the activity is small. If the intent of an exercise prescription is to hold the subject below his or her anaerobic threshold, then the "general" and "respiratory" sensations may be too light to allow an accurate self-monitoring. On the other hand, local muscular sensations around the anaerobic threshold seem in the optimum range for the self-regulation of effort (13-16 units on the Borg scale). Future research should thus focus on the possibility of controlling exercise prescriptions through the perceived intensity of muscular effort, rather than attempting to perceive a light and fallible respiratory target.

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