

Maximal oxygen deficit of sprint and middle distance runners

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Abstract. Anaerobic energy capacity was evaluated by maximal oxygen deficit (MOD) as well as by blood gas and muscle biopsy variables during short exhausting running in six recreational (RR) and eight competitive sprint and middle distance runners (SMDR). On 3 days runs to exhaustion were executed. Two runs were performed at a treadmill gradient of 15% at speeds which resulted in exhaustion after approximately 1 ($R_{15\%,1\text{min}}$) and 2–3 min ($R_{15\%,2-3\text{min}}$), respectively. On the 3rd day, the subjects ran with the treadmill at a gradient of 1% at a speed which caused exhaustion after 2–3 min ($R_{1\%,2-3\text{min}}$). The runner performance was assessed from 400 m [RR, median 64.8 (range 62.2–69.6) s; SMDR, median 49.4 (range 48.5–52.0) s] and 800 m [RR, median 158.8 (range 153.3–170.2) s; SMDR, median 115.2 (range 113.3–123.3) s] track times. Muscle biopsies from gastrocnemius muscle were obtained before and immediately after $R_{15\%,2-3\text{min}}$, from which muscle lactate and creatine phosphate (CP) concentrations, fibre type distribution, capillaries per fibre, total lactate dehydrogenase (LDH) activity and the LDH isoenzyme pattern were determined. The MOD increased with the treadmill gradient and duration. During both treadmill and track runs, SMDR performance was superior to that of RR, but no significant differences were observed with respect to MOD, muscle fibre type distribution, total LDH activity, its iso-enzyme pattern, changes in muscle lactate or CP concentrations. However, after treadmill runs, peak venous lactate concentration and partial pressures of carbon dioxide were higher, and pH lower in SMDR. Also the number of capillaries per muscle fibre and the maximal oxygen uptake were larger in SMDR. These findings would suggest that the superior performance of SMDR depended more on their aerobic than on their anaerobic capacity.

Key words: Anaerobic metabolism – Muscle fibre types – Muscle lactate dehydrogenase – Muscle lactate – Training

Introduction

Anaerobic capacity has been expressed as the accumulated or maximal oxygen deficit (MOD; Medbø and Burgers 1990; Scott et al. 1991). The MOD has been shown to increase until exercise has a duration of more than 2 min (Medbø et al. 1988), and with a treadmill gradient up to 15%, and the thus defined MOD to be larger in 400-m runners compared to anaerobically untrained subjects (Olesen 1992). Of the anaerobic energy release glycolysis has been found to be the largest and most variable part (Karlsson 1971; Nevill et al. 1989; Saltin and Gollnick 1983). Lactate and pyruvate concentrations similar to those of human skeletal muscle have been shown to inhibit lactate dehydrogenase activity (LDH) in vitro (Karlsson et al. 1974), and by way of its iso-enzyme pattern, it has been found that LDH can limit lactate formation and in turn short term performance (Tesch 1979). Accordingly, strength and sprint-trained athletes have been shown to have high, and middle distance runners similar LDH activity and percentage of the “muscle type” (LDH₄₋₅) iso-enzyme as untrained subjects (Costill et al. 1976; Karlsson et al. 1975). It has been thought that this may reflect that LDH and its iso-enzyme pattern is related to the percentage of fast twitch (FT) muscle fibres (Costill et al. 1976; Karlsson et al. 1975; Sjödin et al. 1976; Tesch 1979).

The purpose of this study was to determine if MOD for running in 400–1500 m runners (sprint and middle distance, SMDR) is larger than in anaerobically untrained recreational runners (RR). Furthermore, we evaluated whether the time it takes to reach MOD is influenced by intense training. Thus, competitive SMDR and RR were compared with respect to MOD, muscle lactate and creatine phosphate (CP) concentrations, LDH as well as to its iso-enzyme pattern in the gastrocnemius muscle. Venous blood gas variables were obtained after exercise.

Methods

Subjects. The subjects included six RR who had no record of regular anaerobic training for at least 5 years. Three SMDR ran the 400 m, while five competed in 800–1500 m track events (Table 1). For median 4.5 (range 2–12) years the SMDR group had carried out intense short interval training and were assessed at the end of the season. In addition, two of the SMDR won a national championship (400 m and 400-m hurdles).

Procedure. To establish a linear relationship between submaximal oxygen uptake ($\dot{V}O_2$) and treadmill speed for estimation of energy demand for the exhausting runs, treadmill runs at gradients of 1% and 15% were performed on different days (Fig. 1 and 2). Five to six submaximal runs with increasing treadmill speed were separated by rest periods of 3–7.5 min. Heart rate (HR) and $\dot{V}O_2$ were averaged for the last 2 min of each 6-min period of exercise. If in the established relationship $r < 0.99$ and/or $P > 0.01$, the subjects were re-evaluated on another day.

Separated by 2 to 6 days MOD was determined at a gradient of 15% using two speeds which caused exhaustion after about 1 min ($R_{15\%, 1\text{min}}$) and 2–3 min ($R_{15\%, 2-3\text{min}}$). Also a gradient of 1% was used with a speed leading to exhaustion after 2–3 min ($R_{1\%, 2-3\text{min}}$; Olesen 1992). Before the exhausting runs, the subjects warmed-up for 10 min on a horizontal treadmill at 8–10 $\text{km}\cdot\text{h}^{-1}$ followed by at least 10 min of recovery. On a sign from

one of the investigators they stepped on to the treadmill, which was moving at the predetermined velocity. The $\dot{V}O_2$ and HR were measured continuously. Blood samples were collected anaerobically from a catheter in an arm vein using a QS90 arterial blood sampler (Radiometer, Copenhagen, Denmark) before running, at exhaustion, and every other minute for 10 min of recovery.

Energy demand for the exhausting run was calculated by extrapolation of the relationship between $\dot{V}O_2$ and running speed, and related to maximal oxygen uptake ($\dot{V}O_{2\text{max}}$). The MOD was the difference between total energy demand and accumulated $\dot{V}O_2$, and expressed per kilogram body mass. The oxygen stored in blood and muscle of approximately 6 $\text{ml}\cdot\text{kg}^{-1}$ body mass (Medbø et al. 1988) was included in the calculation. Running economy was $\dot{V}O_2$ per kilogram body mass at velocities of 7 $\text{km}\cdot\text{h}^{-1}$ (15%) and 15 $\text{km}\cdot\text{h}^{-1}$ (1%).

The RR performed two track runs on separate days. After a 10-min warm-up followed by 10 min of recovery, they ran 400 or 800 m in random order. For SMDR their latest track results were used. The $\dot{V}O_{2\text{max}}$ was determined on a separate day as a plateau in $\dot{V}O_2$ with increasing treadmill speed or gradient. Ventilation and $\dot{V}O_2$ were obtained by an Ergo-oxyscreen apparatus (Jäger, Würzburg, Germany). During the exhausting runs, Douglas bags were used (Secher et al. 1974). The HR was monitored by a Sportstester PE 3000 (Polar, Kempele, Finland). Body fat was estimated from skinfold measurements (Durnin and Womersley

Table 1. Characteristics of six recreational (RR) and eight sprint or middle distance runners (SMDR)

	Treadmill gradient (%)	RR median (range)	SMDR median (range)
Age (years)		28 (22–30)	23 (19–33)
Height (cm)		181 (174–189)	185 (178–194)
Body mass (kg)		80 (64–91)	71 (68–89)
Body fat (%)		18.0 (14.6–20.0)	9.2 (7.3–14.2)*
$\dot{V}O_{2\text{max}}$ ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$)		57.8 (49.5–62.0)	72.3 (61.2–82.4)*
Running economy ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$)	1	52.9 (51.7–62.8)	51.7 (48.5–52.8)
	15	52.0 (48.8–56.0)	53.2 (45.0–53.2)
Y intercept of regression lines ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$)	1	5.4 (0.0–9.72)	2.6 (–1.0–11.1)
	15	0.2 (–6.5–8.4)	15.0 (–1.0–28.3)*
Slope of regression lines ($\text{ml}\cdot\text{kg}^{-1}\cdot\text{min}^{-1}$)	1	3.4 (2.8–3.5)	3.1 (2.6–3.5)
	15	7.3 (6.6–7.9)	5.6 (3.8–6.7)*
400 m (s)		64.8 (62.2–69.6)	49.4 (48.5–52.0)*
800 m (s)		158.8 (153.3–170.2)	115.2 (113.3–123.3)*
Fibre type distribution (%)	ST	58 (52–79)	58 (30–94)
	FTa	29 (14–43)	37 (6–61)
	FTb	6 (2–17)	1 (0–9)
Capillaries per fibre		2.4 (2.1–2.5)	2.7 (2.3–3.1)*

In comparison with RR and SMDR, * $P \leq 0.05$; $\dot{V}O_{2\text{max}}$, maximal oxygen uptake; ST, FT, slow twitch, fast twitch muscle fibres, respectively. Running economy, oxygen uptake when running at

15 and 7 $\text{km}\cdot\text{h}^{-1}$ at gradients of 1% and 15%, respectively. Capillaries per fibre, RR $n = 5$, SMDR $n = 7$

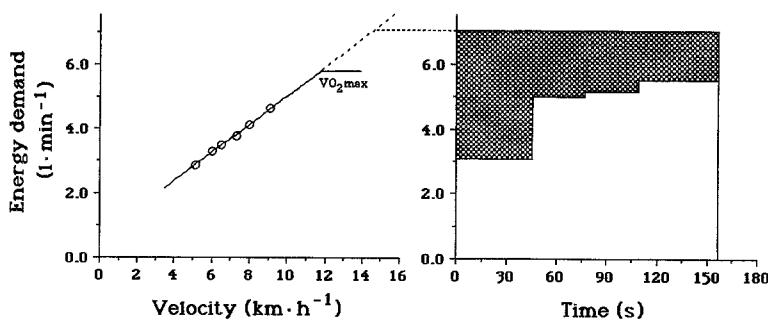


Fig. 1. Diagram of the calculation procedure for maximal oxygen deficit. *Left*, extrapolation of the relationship between oxygen uptake and velocity. *Right*, exhausting run with the energy demand calculated according to the established relationship (*left*). The maximal oxygen deficit (*double hatched*) is the difference between the thus defined total energy demand and maximal oxygen uptake ($\dot{V}O_{2\text{max}}$; *open area*)

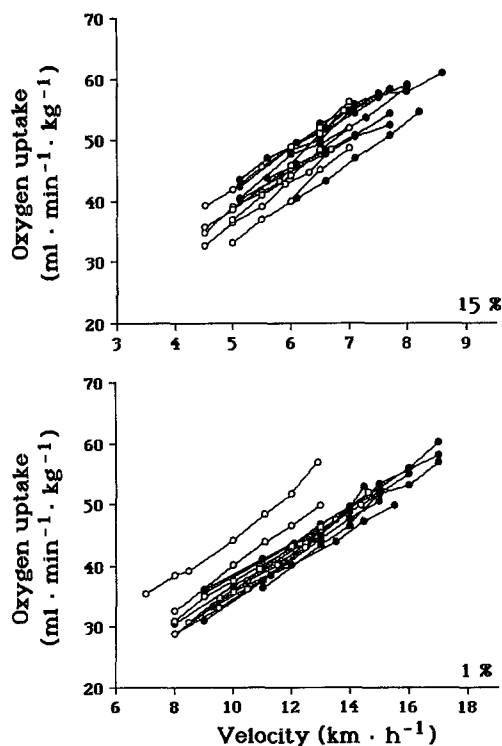


Fig. 2. Oxygen uptake vs running velocity at treadmill gradients of 1% and 15%. ○ Recreational runner; ● sprint or middle distance runner

1974). Venous partial pressure of carbon dioxide (PCO_2), pH and bicarbonate concentration ($[HCO_3^-]$) were determined on an ABL-4 apparatus (Radiometer, Copenhagen, Denmark). Lactate concentration was measured using whole blood (GM-7 Analox, London, UK).

Bergström needle biopsies were obtained from the lateral portion of the gastrocnemius muscle before and immediately after the $R_{15\%, 2-3\text{min}}$. One portion of the resting muscle sample was mounted in OCT embedding medium for histochemical evaluation and frozen in isopentane cooled by liquid nitrogen. A second piece and the biopsy taken at exhaustion were frozen immediately in nitrogen and stored at -80°C .

Table 2. Characteristics of exhausting runs

		Velocity ($\text{km} \cdot \text{h}^{-1}$)	Time to exhaustion (min:s)	Energy demand ($\text{ml} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$)	Relative intensity (%)	Maximal O_2 deficit ($\text{ml} \cdot \text{kg}^{-1}$)
$R_{15\%, 1\text{min}}$	RR	median 14.1 range (12.0–15.4)	1:02 (0:56–1:10)	99.3 (84.6–110.3)	176 (171–200)	64.8 (57.3–80.1)
	SMDR	median 18.0 ^a range (15.4–18.8)	1:04 (0:51–1:15)	114.6 (88.9–126.8)	154 ^a (123–207)	68.3 (44.4–80.5)
$R_{15\%, 2-3\text{min}}$	RR	median 10.7 range (9.8–11.3)	2:28 (1:48–3:07)	82.3 ^b (69.8–83.2)	138 (133–149)	86.8 ^b (70.8–94.4)
	SMDR	median 14.4 ^a range (12.3–14.8)	2:19 (1:57–2:37)	88.9 ^{a, b} (80.0–97.5)	128 ^a (110–144)	82.9 ^b (52.6–104.6)
$R_{1\%, 2-3\text{min}}$	RR	median 18.2 range (17.5–19.5)	2:28 (2:13–2:38)	66.4 (59.2–73.1)	120 (104–123)	53.0 ^c (48.9–57.3)
	SMDR	median 24.0 ^a range (23.0–24.5)	2:26 (2:00–3:01)	76.2 ^a (71.0–84.5)	108 (99–115)	52.2 ^c (33.9–74.6)

$R_{15\%, 1\text{min}}$, Exhaustion reached after 1 min running at gradient of 15%; $R_{15\%, 2-3\text{min}}$, exhaustion reached between 2nd and 3rd min of running at a gradient of 15%; $R_{1\%, 2-3\text{min}}$, exhaustion reached between 2nd and 3rd min of running at a gradient of 1%. Rela-

The LDH and its iso-enzyme pattern were determined for the biopsy obtained at rest after separation of connective tissue by eye. Following homogenization in 1-ml 0.9% NaCl and centrifugation, LDH was assessed by spectrophotometry of the supernatant on a Cobas Bio apparatus (Hoffmann and Roche, Switzerland) at 37°C (Keiding et al. 1974). For separation of iso-enzymes, modified cellulose acetate (Cellogel, Chemetron, Italy) electrophoresis was used (Raabo 1963). Muscle lactate and CP concentrations were determined on freeze dried samples of the biopsy obtained at exhaustion by a fluorometric assay (Lowry and Passoneau 1972). The OCT mounted biopsy was cut in 10- μm transverse sections at -20°C and stained for myofibrillar adenosine triphosphatase (ATPase; Padykula and Herman 1955) to obtain classification of slow twitch (ST), FTa, and FTb fibres (Brooke and Kaiser 1970). The amylose periodic acid-shift PAS method was used to visualize capillaries (Andersen 1975) and evaluated using a COMFAS apparatus (Scan Beam, Hadsund, Denmark).

Statistics. Mann-Whitney's test was used to evaluate differences between the two groups. The three exhausting runs were compared by Friedman's two-way analysis of variance and deviations located by Wilcoxon's signed-rank test. Regression lines were calculated by the least squares method (Sigmaplot 4.0). The estimate of energy demand for the exhausting run was calculated with the 95% confidence interval for the regression line between $\dot{V}O_2$ and velocity as extrapolated to the applied velocity. Analysis of covariance was used to evaluate differences in regression lines between groups. Significance was chosen to represent a value of P equal to or less than 0.05.

Results

SMDR versus RR

The SMDR were leaner, had a larger $\dot{V}O_{2\text{max}}$ and a greater number of capillaries per muscle fibre, and ran faster during treadmill and track runs than RR, but there was no significant difference in running economy between the two groups of subjects (Table 1). However, for SMDR the slope of the regression lines was smaller and the Y intercept larger at a gradient of 15% $1.5\Delta(\text{muscle lactate}) + \Delta(\text{CP}) + \Delta(\text{ATP})$ (Bangsbo et al. 1987) than RR, but between groups there was no significant

relative intensity (energy demand/ $\dot{V}O_{2\text{max}}$) $\times 100$. In comparison with RR, $P \leq 0.05$; $R_{15\%, 2-3\text{min}}$ vs $R_{15\%, 1\text{min}}$, ^b $P \leq 0.05$; $R_{1\%, 2-3\text{min}}$ vs $R_{15\%, 2-3\text{min}}$ ^c $P \leq 0.05$

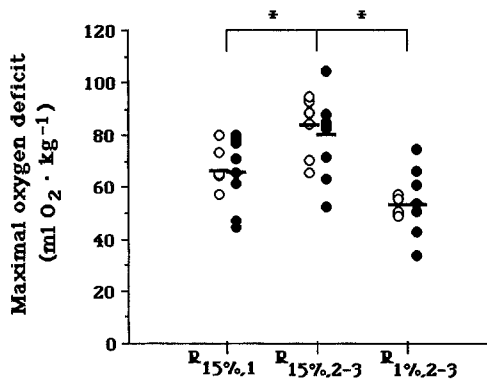


Fig. 3. Individual data and means for maximal oxygen deficit. $R_{15\%.1\text{min}}$, Exhaustion reached after 1 min running at a gradient of 15%; $R_{15\%.2-3\text{min}}$, exhaustion reached between 2nd and 3rd min of running at a gradient of 15%; $R_{1\%.2-3\text{min}}$, exhaustion reached between 2nd and 3rd min of running at a gradient of 1%. ○ Recreational runner; ● sprint or middle distance runner. Comparison between runs. * $P \leq 0.05$

difference in time to exhaustion (Table 2). Also, there was no significant difference in calculated energy demand during $R_{15\%.1\text{min}}$, but during $R_{15\%.2-3\text{min}}$ and $R_{1\%.2-3\text{min}}$ energy demand was larger for SMDR. The RR ran at a larger percentage of their $\dot{V}O_{2\text{max}}$, while the O_2 kinetics expressed relative to $\dot{V}O_{2\text{max}}$ and MOD (Fig. 3) were similar for the two groups of subjects.

Peak blood lactate concentration and PCO_2 were larger and the decrease in pH more pronounced in SMDR than in RR (Table 3). The lowest pH was observed immediately after exhaustion in SMDR, but after 2 (0–6) min for RR, and it remained reduced for 10 min of recovery.

After the exhausting exercise muscle lactate [median 55 (range 36–102) vs median 76 (range 57–126) $\text{mmol} \cdot \text{kg}^{-1}$ dry mass], CP [median 29.5 (range 13.3–

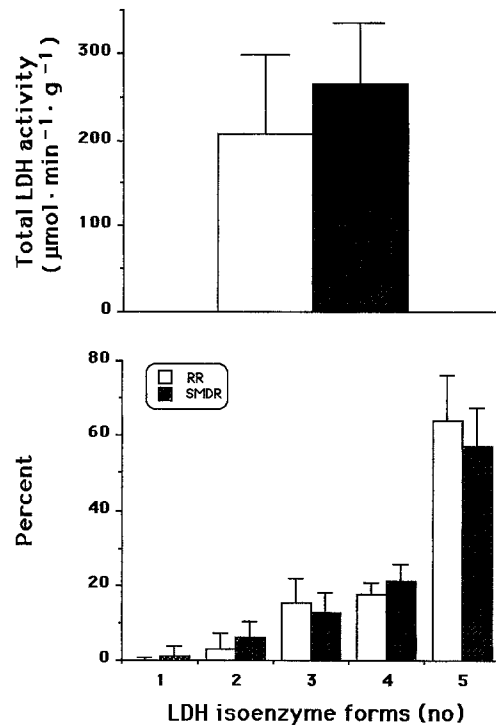


Fig. 4. Mean and SD for total muscle lactate dehydrogenase (LDH) activity, and LDH iso-enzyme distribution. RR, Recreational runner; SMDR, sprint or middle distance runner. No significant differences were found

50.8) vs median 32.8 (range 26.7–39.8) $\text{mmol} \cdot \text{kg}^{-1}$ dry mass] and water content [median 75.8 (range 75.5–76.4) vs median 75.9 (range 71.0–77.0)%] were similar for SMDR and RR. Total LDH activity and the iso-enzyme distribution were also similar for the two groups of subjects. The dominant iso-enzyme was LDH₅ (Fig. 4), which correlated to the percentage of FT muscle fibres ($r=0.61$).

Table 3. Peak venous blood lactate concentration, pH partial pressure of carbon dioxide (PCO_2), and bicarbonate concentration ($[HCO_3^-]$) after exhausting running

		Lactate ($\text{mmol} \cdot \text{l}^{-1}$)	pH	PCO_2 (kPa)	$[HCO_3^-]$ ($\text{mmol} \cdot \text{l}^{-1}$)
$R_{15\%.1\text{min}}$	RR	median 9.6 range (7.2–12.0)	7.16 (7.11–7.26)	8.8 (5.8–12.6)	13.0 (10.0–13.2)
	SMDR	median 11.5 range (10.4–14.4)	7.02 ^a (6.89–7.06)	12.9 ^a (11.8–16.1)	11.0 (8.8–14.5)
$R_{15\%.2-3\text{min}}$	RR	median 12.2 range (7.5–13.2)	7.07 ^b (6.91–7.20)	10.3 (7.6–14.5)	11.9 (9.9–15.1)
	SMDR	median 12.9 range (9.5–16.0)	6.92 ^b (6.82–7.07)	14.0 ^a (10.1–17.0)	10.7 (7.6–16.4)
$R_{1\%.2-3\text{min}}$	RR	median 8.5 range (7.8–12.6)	7.15 ^c (7.04–7.23)	8.7 (7.6–11.6)	13.1 (9.6–15.5)
	SMDR	median 13.3 ^{a,b} range (10.8–17.2)	6.88 ^a (6.83–7.08)	15.3 ^a (10.4–17.7)	10.7 (6.2–12.4)
Mean ^d	RR	10.4 range (7.9–11.8)	7.13 (7.00–7.23)	9.2 (7.4–12.9)	13.0 (10.1–13.2)
	SMDR	12.8 ^a range (11.4–14.5)	6.95 ^a (6.89–7.00)	13.6 ^a (12.5–16.1)	11.0 (9.2–13.4)

For abbreviations see Table 2. In comparing with RR, ^a $P \leq 0.05$; in comparing with $R_{15\%.1\text{min}}$, ^b $P \leq 0.05$; $R_{1\%.2-3\text{min}}$ in comparison with $R_{15\%.2-3\text{min}}$, ^c $P \leq 0.05$, ^d mean of three runs

Comparison between runs

For both groups of subjects the $R_{1\%,2-3\text{min}}$ and $R_{15\%,1\text{min}}$ MOD was median 64 (range 52–85)% and median 83 (range 70–95)%, respectively, of that reached during $R_{15\%,2-3\text{min}}$ (Table 2). The 95% confidence interval for energy demand was median 18 (range 7–42) ml $\text{O}_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ [corresponding to median 18 (range 7–44)% of the energy demand] during $R_{15\%,1\text{min}}$. For $R_{1\%,2-3\text{min}}$ it was median 6 (range 5–20) ml $\text{O}_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ [median 9 (range 3–18)%] and for $R_{15\%,2-3\text{min}}$ median 12 (range 4–32) ml $\text{O}_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$ [median 15 (range 4–39)%].

Blood pH was lower after $R_{15\%,2-3\text{min}}$ than after $R_{15\%,1\text{min}}$, and peak blood lactate concentration tended to be larger. Compared to pH, the lowest $[\text{HCO}_3^-]$ was observed late in recovery (Fig. 5). The PCO_2 was largest at exhaustion, and decreased to resting levels after 4–6 min. Peak blood lactate concentration and pH were correlated ($r=0.84$), but unrelated to MOD. Also, there was no significant correlation between MOD and muscle lactate ($r=0.34$). The 400 and 800-m track performances correlated to $\dot{V}\text{O}_{2\text{max}}$ per kilogram body mass ($r=0.72$ and 0.87 , respectively), but not to MOD.

Discussion

Both during treadmill and track runs the performance of SMDR was superior to that of RR. This difference was related to aerobic capacity as expressed by $\dot{V}\text{O}_{2\text{max}}$ and to the number of capillaries per muscle fibre, but not to anaerobic energy release as indicated by the MOD or by the muscle blood lactate and CP concentrations. While also LDH and its iso enzyme pattern were similar between the two groups of subjects, blood gas variables indicated a larger anaerobic energy release in SMDR. These findings may be limited by the methods used as well as by the selection of the subjects.

Evaluation of anaerobic capacity

The MOD increased from 1 to 2–3 min of exercise (Medbø et al. 1988) and was about 50% larger when running at an inclination of 15% than at 1% (Olesen 1992). With a confidence interval for energy demand of 15% when the largest MOD was obtained, there were no significant differences between groups with respect to MOD and the percentage of MOD obtained after 1 min. These results should be considered in the light that the most critical assumption for the calculation of MOD is that mechanical efficiency is independent of exercise intensity, but it is very likely that this was not fully fulfilled. This has been illustrated during swimming, where MOD is large in swimmers with a large $\dot{V}\text{O}_2$ during submaximal swimming, indicating that MOD underestimates anaerobic capacity in proportion to swimming economy (Olesen et al. submitted

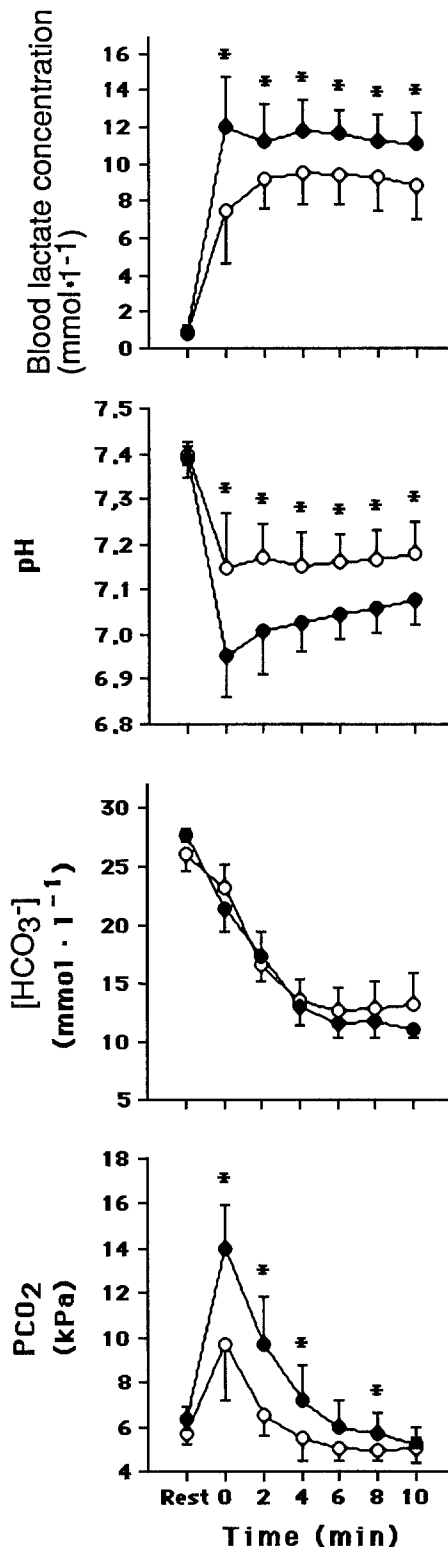


Fig. 5. Mean and SD for blood lactate concentration, pH, bicarbonate concentration ($[\text{HCO}_3^-]$), and venous partial pressure of carbon-dioxide (PCO_2) at rest and during 10 min of recovery. Values are averages for three exhausting runs. ○ Recreational runner; ● sprint or middle distance runner. Comparison between groups, * $P \leq 0.05$

for publication). However, compared to swimming, variation in running economy was small.

A further problem with the calculation of MOD is that at high submaximal work intensities a true steady-state $\dot{V}O_2$ is not regularly established as $\dot{V}O_2$ of the working muscle may increase (Henson et al. 1989; Poole et al. 1991). With such an increase in $\dot{V}O_2$, efficiency is reduced from approximately 30% to a value as low as 20% at high exercise intensities. In this study $\dot{V}O_2$ increased with running velocity close to a power of one (that is linearly) at treadmill gradients of both 1% and 15%, while it has been reported to increase curvilinearly (during cycling), when the slow phase $\dot{V}O_2$ was taken into account (Roston et al. 1987).

The two groups of subjects had similar muscle lactate and CP concentrations, but in the SMDR blood lactate concentrations and PCO_2 were higher, and pH lower after exercise. Variation in muscle versus blood lactate concentration may reflect lactate release from other muscles, differences in the dilution space for lactate and the muscle mass involvement in exercise (Rasmussen et al. 1991). Lactate release from the active muscles may have been larger in SMDR, since their $\dot{V}O_{2max}$ (reflecting cardiac output) and capillaries per fibre were larger (Juel et al. 1990). Furthermore, training has been shown to increase the capacity to transport lactate in rat skeletal muscle (Pilegaard et al. 1993), and the exercise muscle blood concentration difference is large in trained compared to untrained subjects (Karlsson 1971).

At exhaustion anaerobic energy release is estimated from muscle lactate and CP concentrations as $1.5\Delta(\text{muscle lactate}) + \Delta(CP) + \Delta(ATP)$ (Bangsbo et al. 1990; Cheetham et al. 1986). With a resting muscle blood lactate concentration of $2 \text{ mmol} \cdot \text{kg}^{-1}$ wet mass, a CP concentration of $20 \text{ mmol} \cdot \text{kg}^{-1}$ wet mass, and a decrease in the adenosine triphosphate (ATP) storage of $2 \text{ mmol} \cdot \text{kg}^{-1}$ wet mass, respectively (Karlsson 1971; Saltin and Gollnick 1983), total anaerobic energy release was approximately $36 \text{ mmol ATP} \cdot \text{kg}^{-1}$ muscle wet mass. This value is low compared to that shown for exhausting knee extension (Bangsbo et al. 1990), but similar to the value derived for 30-s sprint running (Cheetham et al. 1986). Assuming an exercising muscle mass approximately 25% of body mass and that 1 mol O_2 is equivalent of 6.5 mol ATP (Karlsson 1971; Medbø et al. 1988), anaerobic energy turnover corresponded to $29 \text{ ml } O_2 \cdot \text{kg}^{-1}$ body mass. The amount of lactate that left the muscle is not considered in this calculation, but may be of little importance during whole body exercise (Juel et al. 1990; Secher et al. 1977). This would suggest that the gastrocnemius muscle may not be working at a maximal intensity during uphill running (Costill et al. 1974).

Selection of subjects

A high MOD has been reported in 400-m runners (Olesen 1992) and the largest MOD value ($105 \text{ ml } O_2 \cdot \text{kg}^{-1}$) has been determined in such a runner. Ac-

cordingly, combining results from the present study with those from Olesen (1992), who used the same protocol, demonstrate a MOD of $95 \text{ ml } O_2 \cdot \text{kg}^{-1}$ for the 400-m runners ($n=7$), $79 \text{ ml } O_2 \cdot \text{kg}^{-1}$ for the 800–1500 m runners ($n=6$) and a similar value of $74 \text{ ml } O_2 \cdot \text{kg}^{-1}$ for RR ($n=11$).

In conclusion, MOD was similar for SMDR and RR, and the superior performance of SMDR was related more to their large aerobic capacity as also indicated by their dense muscle capillary supply. Yet, blood lactate concentrations was high and pH low in SMDR, while their metabolites in gastrocnemius muscle were similar. These findings could reflect that a large anaerobic capacity distinguishes 400-m runners rather than 800–1500-m runners from RR.

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