Dependence of the maximal lactate steady state on the motor pattern of exercise

R Beneke, R M Leithäuser, M Hütler

Abstract

Background—Blood lactate concentration (BLC) can be used to monitor relative exercise intensity. The highest BLC representing an equilibrium between lactate production and elimination is termed maximal lactate steady state (MLSS). MLSS is used to discriminate qualitatively between continuous exercise, which is limited by stored energy, from other types of exercise terminated because of disturbance of cellular homeostasis.

Aim—To investigate the hypothesis that MLSS intraindividually depends on the mode of exercise.

Methods—Six junior male rowers (16.5 (1.4) years, 181.7 (3.1) cm, 69.8 (3.3) kg) performed incremental and constant load tests on rowing and cycle ergometers. Measurements included BLC, sampled from the hyperaemic ear flap, heart rate, and oxygen uptake. MLSS was defined as the highest BLC that increased by no more than 1.0 mmol/l during the final 20 minutes of constant workload.

Results—In all subjects, MLSS was lower ($p \leq 0.05$) during rowing (2.7 (0.6) mmol/l) than during cycling (4.5 (1.0) mmol/l). No differences between rowing and cycling were found with respect to MLSS heart rate (169.2 (9.3) *v* 172.3 (6.7) beats/min), MLSS workload (178.7 (29.8) *v* 205.0 (20.7) W), MLSS intensity expressed as a percentage (63.3 (6.6)% *v* 68.6 (3.8)%) of peak workload (280.8 (15.9) *v* 299.2 (28.4) W) or percentage (76.4 (3.4)% *v* 75.1 (3.0)%) of peak oxygen uptake (60.4 (3.4) *v* 57.2 (8.6) ml/kg/min).

Conclusions—In rowing and cycling, the MLSS but not MLSS workload and MLSS intensity intraindividually depends on the motor pattern of exercise. MLSS seems to decrease with increasing mass of the primarily engaged muscle. This indicates that task specific levels of MLSS occur at distinct levels of power output per unit of primarily engaged muscle mass.

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minutes and is considered to discriminate qualitatively between training methods in which continuous exercise is limited by stored energy from others which have to be terminated because of disturbance of cellular homeostasis.

In top athletes performing their specific type of exercise, MLSS was found to be interindividually different.² The latter study was performed on the basis of the fact that specific training sessions resulted in BLCs that obviously differed from generally expected values.^{3–9,10} However, a comparison of top athletes performing their specific exercises cannot effectively discriminate between effects related to specific tasks, personal factors, and/or possible complex adaptations to a long lasting training process.

The hypothesis that the MLSS depends on the specific task itself was investigated by an intraindividual analysis of rowing and cycling ergometry in junior athletes who were able to perform, and were used to performing, both rowing and cycling on a regular basis but were not highly specialised top athletes.

Methods

SUBJECTS AND PROCEDURES

The intraindividual comparison of MLSS in rowing and cycling was conducted in six junior male rowers (age 16.5 (1.4) years; height 181.7 (3.1) cm; body mass 69.8 (3.3) kg; means (SD)) of regional or national level. They had carried out 6–10 hours of systematic training a week for 1–2 years, including specific training in a boat and on a rowing ergometer and non-specific exercises such as cycling, running, and power lifting. The test period was during the winter when training in a boat was the exception because of weather conditions. No subject was receiving pharmacological or dietetic treatment. Informed consent was obtained after explanation of the nature and risks involved in participation in the experiments, which conformed to internationally accepted policy statements regarding the use of human subjects.

EXERCISE TESTING

The subjects performed incremental and constant load tests on a rowing ergometer (Gjessing; Empacher, Eberbach, Germany) with a brake load of 27 N and on a cycle ergometer (Elema Schönander 380, Siemens, Germany). All tests were conducted at similar times in the afternoon on separate days at least two hours after a light meal. Time between separate testing sessions was 48–72 hours. The subjects were instructed not to engage in strenuous activity during the day before an exercise test.

Sports Medicine, Free University, Berlin, Germany
R Beneke
M Hütler

Rehabilitationsklinik Elbe-Saale, Barby, Germany
R Beneke

xx-well.com AG, Berlin
R Beneke

LMC Laboratory, Berlin
R M Leithäuser

Correspondence to:
Dr Beneke, Brauhofstr 1,
10587 Berlin, Germany
rabe94@zedat.fu-berlin.de

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Blood lactate concentration (BLC) is a widely used variable for estimating relative exercise intensity.^{1–6} The maximal lactate steady state (MLSS) corresponds to the highest constant workload that can be maintained over time without continuous blood lactate accumulation.^{5–7,8} MLSS intensity corresponds to intensive endurance training normally lasting 20–60

ERGOMETRY

The initial rowing ergometer workload was 145 W and was increased by 35 W every three minutes. After every work stage, the test was interrupted by a 30 second break for blood sampling. The cycle ergometer test started with 100 W and was increased by 50 W every third minute. Blood sampling was conducted at the end of every work stage. All incremental load tests were finished at individual maximal power outputs indicated by volitional fatigue after strong vocal encouragement.

All constant load tests lasted 30 minutes except those that were terminated because of volitional fatigue. In rowing, the stroke frequency was 25–32 strokes/min. Cycle ergometry was performed with individual constant pedalling rates of at least 90/min. According to a previous procedure,² the first constant workload corresponded to a BLC of 2.0–2.5 mmol/l measured during the incremental load test in rowing. In cycle ergometry, the analogous BLC was 4.0 mmol/l. Constant load tests with 5–10% higher or lower workloads were conducted on subsequent days until MLSS was verified. This resulted in seven to 12 constant load tests per subject. MLSS was defined as the highest BLC that increased by no more than 1.0 mmol/l during the final 20 minutes of a constant workload. The MLSS was calculated as the mean BLC measured at 15, 20, 25, and 30 minutes of the MLSS workload.¹¹

BLOOD LACTATE CONCENTRATION

Capillary blood samples (20 µl) were taken from the hyperaemic ear flap (Finalgon forte, Thomae, Biberach, Germany). During incremental load tests, blood was drawn before the test and at the end of each stage. During the constant load tests, the BLC was measured before and at the end of every 5th minute. The BLC was analysed by an enzymatic photometric method (Boehringer, Mannheim, Germany). Coefficients of variation for repeat analyses of identical samples were less than 5%.¹²

HEART RATE

Heart rate was monitored continuously throughout all tests (Sport tester PE 3000; Polar, Oy; Finland). Data corresponding to the time of blood sampling were analysed.

OXYGEN UPTAKE

Oxygen uptake was determined with a portable spirometric system (K2; Cosmed, Rome, Italy) in 15 second intervals. Before each test, the device was calibrated according to the manufacturer's instructions. The coefficient of reliability for oxygen uptake measurements with such a system has been reported to be about 0.99.¹³ Compared with other methods of measuring oxygen uptake, the K2 showed similar^{13 14} or slightly lower values of oxygen uptake at levels above 2.7 l/min.¹⁵

METABOLIC POWER AND MECHANICAL EFFICIENCY

According to a previously published procedure,¹⁶ the net metabolic power was calculated as follows: metabolic power (W) = oxygen

uptake above rest (ml/s) × caloric equivalent (J/ml) + net lactate production (mmol/l/s) × oxygen-lactate equivalent (ml/kg/mmol) × body mass (kg) × caloric equivalent (J/ml).

Oxygen-lactate equivalent and caloric equivalent were set to 3.0 ml/mmol/kg¹⁷ and 21.131 J/ml.¹⁸ Mechanical efficiency was calculated from mechanical power per metabolic power times 100.

STATISTICAL ANALYSIS

Data are reported as mean (SD). Differences within subjects were determined by the Wilcoxon test. Relations between variables were examined by linear regression analysis. For all statistics, the significance level was set at $p \leq 0.05$.

Results

In all subjects, MLSS was lower ($p \leq 0.05$) during rowing (2.7 (0.6) mmol/l) than during cycling (4.5 (1.0) mmol/l) (fig 1). No difference ($p > 0.05$) was found between rowing and cycling with respect to the workload identified to result in MLSS (178.7 (29.8) v 205.0 (20.7) W). No BLC steady state was observed at constant workloads about 5.5% higher than MLSS workloads in rowing and cycling (fig 2).

Oxygen uptake at MLSS (46.2 (4.0) v 43.0 (7.0) ml/kg/min) and heart rate at MLSS (169.2 (9.3) v 172.3 (6.7) beats/min) were not different in rowing and cycling ($p > 0.05$). Also the corresponding relative exercise intensities expressed as a percentage (63.3 (6.6)% v 68.6 (3.8)%) of peak workload (280.8 (15.9) v 299.2 (28.4) W) or percentage (76.4 (3.4)% v 75.1 (3.0)%) of peak oxygen uptake (60.4 (3.4)

Figure 1 Blood lactate concentration (BLC) response to maximal lactate steady state workload in rowing and cycle ergometry.

Figure 2 Blood lactate concentration (BLC) response to relative workload intensities about 5.5% higher than maximal lactate steady state workload in rowing and cycle ergometry. In cycling, only five subjects were able to continue for 25 minutes (*) and four subjects were able to cycle for 30 minutes (†).

Figure 3 Correlation between maximal lactate steady state (MLSS) $\dot{V}O_2$ and peak $\dot{V}O_2$ in rowing and cycle ergometry.

v 57.2 (8.6) ml/kg/min) were not different in rowing and cycling ($p > 0.05$). Peak BLC reached after termination of the incremental load test did not differ significantly between rowing (11.1 (2.3) mmol/l) and cycling (10.0 (1.8) mmol/l). Consequently the values of metabolic power at MLSS workload and at peak workload of 1016 (113) W and 1595 (270) W in rowing and of 938 (165) W and 1508 (294) W in cycling were not different ($p > 0.05$). The corresponding biomechanical efficiencies at MLSS were 17.6 (1.9)% v 22.1 (2.2)% ($p \leq 0.05$) and 17.9 (2.5)% v 20.4 (3.8)% ($p > 0.05$) at peak workload.

Independently of the type of exercise, correlations ($p \leq 0.05$) were found between MLSS workload and peak workload ($r = 0.88$, $p \leq 0.001$, $y = 1.34x - 194.4$), and between MLSS oxygen uptake and peak oxygen uptake (fig 3).

Discussion

In young, not highly specialised athletes with similar training methods over 1–2 years, the MLSS was intraindividually lower in rowing than in cycle ergometry. In addition, the experiments showed similar results to those for top rank athletes performing only their specific type of exercise.² Thus our results provide strong evidence that the motor pattern of exercise and not other previously discussed modulators, such as subject variation and specific adaptation to exercise training, predominantly causes the observed interindividual divergence of MLSS.

In contrast with the MLSS, the workload at MLSS did not differ between rowing and cycle ergometry. Furthermore, the present data underline and extend results indicating that MLSS intensity expressed as a percentage of the peak workload did not differ between selected sports.² However, it should be taken into consideration that, on traditional rowing ergometers, the body mass is moving backwards and forwards on a rolling seat during each stroke. The corresponding acceleration and deceleration forces cause an additional stroke rate dependent mechanical power output which is not measured. At stroke rates of about 30/min, as in the present study, the corresponding additional power output is about 0.7 W/kg body mass.^{19–20} This would increase MLSS workload and peak workload considerably to about 228 W and 329 W. Metabolic power can be calculated from oxygen uptake

and net lactate production,¹⁶ and biomechanical efficiency from MLSS workload, peak workload, and the corresponding metabolic rates. On the basis of the latter, the contribution to the above correction of the measured rowing workloads would increase the biomechanical efficiency of rowing ergometry from about 18% to about 22%, which is similar to the observed efficiency of cycling. Thus the latter consideration of indirectly measured fractions of mechanical power in rowing would result in higher ($p \leq 0.05$) workload at MLSS and peak workload in rowing compared with cycle ergometry but does not have any effect on the corresponding relative exercise intensity.

The MLSS represents the highest equilibrium between lactate appearance and disappearance in the intravascular compartment, which is underlined by the fact that more than 99% of the metabolic power is provided aerobically in both rowing and cycling and that the corresponding fraction of anaerobic lactate energy is more or less exclusively generated during the initial 5–10 minutes of constant workload (fig 1). However, BLC and thus MLSS does not represent the metabolic state of selected muscles.^{21–22} During exercise, lactate production and elimination may be controlled by the mass of the muscle being exercised.²³ Other organs that contribute to lactate metabolism, such as heart,²⁴ liver,²⁵ and kidneys,²⁶ have a smaller tissue mass or reduced perfusion compared with the skeletal muscle during exercise.²⁷

Lactate production and oxidative lactate clearance is determined by factors such as mass of the primarily engaged skeletal muscle, pattern of intermuscular coordination, and fibre recruitment.^{28–31} These factors appear to be affected by the motor pattern of exercise. Rowing is a combination of leg, trunk, and arm work, which represents more than 85% of the total muscle mass.¹⁹ This is considerably more than the corresponding muscle mass in cycling, which is dominated by leg work. The fact that different levels of MLSS appeared at similar levels of oxygen uptake, relative exercise intensity, and heart rate indicates that, in rowing, the power output per unit of muscle mass is less than in cycling. Assuming that rowing power output is generated by about 85% of the total muscle mass and that the total muscle mass represents about 40% of the body mass, the observed performance would result in a relative power output per kg muscle mass of 9.6 W/kg at MLSS and 13.9 W/kg at peak workload in rowing ergometry. In cycling, which requires work by about 60% of the total muscle mass, the corresponding relative workloads would be 12.2 W/kg at MLSS and 17.8 W/kg at peak workload. In cycling, this muscular exercise intensity is 25–30% higher than the corresponding value in rowing even if the additional rolling work during rowing ergometry is taken into consideration. This underlines and extends previous results showing that the power output per unit muscle mass and the BLC are lower if the mass of the primarily engaged muscle increases.³²

The latter is supported by observations that, at a given level of oxygen uptake and similar total glycogen consumption,^{33–35} the glycogen loss per muscle fibre is lower in running than in cycling^{33,34} and that, at similar exercise intensities, muscular glycolysis is higher during arm cranking than during cycling.³⁶ In addition, glycogen uptake by the legs is reduced if arm exercise is added to the cycle ergometer work.³⁷ Also the force and dynamics of muscular engagement are specific qualities of selected tests. Biomechanical analyses comparing rowing on a boat and rowing on an ergometer²⁰ and kinematic data of cycling at different pedalling rates³⁸ indicated corresponding divergences in force and dynamics per stroke. In cycling, the driving force per stroke and its rating increase at lower pedalling rates.^{39,40} In addition, low pedalling rates cause intensive upper body work. Such variations in the motor pattern of exercises may affect MLSS because glycolysis and pyruvate oxidation depend on the energetic demands of exercise.^{30,31}

Glycolysis can be expected to increase more or less sigmoidally with relative exercise intensity.^{30,31} In contrast, the relation between relative exercise intensity and oxidative metabolism is almost linear.⁴¹ During exercise, lactate production and elimination are determined by exercise intensity and mass of the muscles engaged. In a given mode of exercise, the primarily engaged muscles work with higher exercise intensity than the assisting muscles. If the primarily engaged muscle mass is small, the complementary muscular work is performed by a large muscle mass exercising at low relative intensity. According to the lactate shuttle hypothesis,^{28,29} a large assisting muscle mass may be able to use lactate as fuel for oxidative metabolism if, in the small primarily engaged muscle mass, lactate production is higher than lactate oxidation. Under these conditions, a steady state of BLC may indicate an overall balance between lactate appearance and disappearance in spite of net lactate production by the primarily engaged muscles. With increasing mass of the primarily engaged muscle, the difference in relative exercise intensity between the latter and the assisting muscle mass may decrease. With respect to a steady state of BLC, this may diminish the capacity to compensate net lactate production of the primarily engaged muscles. This may explain why, compared with cycling, lower levels of MLSS in rowing appear to be combined with similar or even higher BLCs at peak workload, indicating a more or less similar fraction of 15% anaerobic lactate energy in rowing and cycling.

The highest MLSS values are observed in speed skating^{2,42} and arm ergometry.⁴³ Obviously, in arm ergometry the mass of the primarily engaged muscles is lower than in cycling. Low pedalling rates and rowing ergometry intensifying arm work resulted in the lowest MLSS values.^{2,7} This seems to be in line with observations that exercise by small muscle masses such as arm ergometry result in higher glycolytic rates of the working muscles possibly through greater sympathoadrenal stimulation

and coactivation.^{36,37,44,45} Therefore the level of MLSS may be negatively related to the mass of the primarily engaged muscles. Consequently, the ratio between the mass of the primarily engaged and assisting muscles may modulate the dynamic steady state between lactate production and elimination and thus the MLSS.

In conclusion, this study supports the hypothesis that the MLSS predominantly depends on the motor pattern of exercise. The differences in MLSS observed during different types of exercise seem to be caused by differences in mass of the primarily engaged muscles. With respect to the latter, MLSS seems to correspond to task specific levels of power output per unit of working muscle. This appears to cause task specific BLC limits, allowing an overall equilibrium between glycolytic production and oxidative consumption of lactate. The latter may explain why the MLSS is negatively related to the mass of the primarily engaged muscles.

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Take home message

The highest BLC representing an equilibrium between lactate production and elimination is termed maximal lactate steady state (MLSS). MLSS seems to decrease with increasing mass of the primarily engaged muscles. This indicates that task specific levels of MLSS occur at distinct levels of power output per unit of primarily engaged muscle mass.