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Plasma Lactate Kinetics during Exercise

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ABSTRACT Oxygen consumption ($\dot{V}_{O_2}$), plasma concentrations ([lact]) and net plasma lactate accumulation rates ($\dot{M}_{Lactate}$) were measured in 6 Thoroughbred horses running on a level treadmill at various speeds. Standardized exercise protocols consisted of a 3 min warm up at 4 m s^{-1}, 3 min rest standing on the treadmill, 2 min at 4 m s^{-1}, 2 min at 7 m s^{-1}, and 3 min at a higher speed (10–17 m s^{-1}), with [lact] measured at the end of the run at each speed. [Lact] remained unchanged from resting concentration at all running speeds below 7 m s^{-1} (1.58±0.33 mmol l^{-1}, mean ± SEM, n=6). At 7 m s^{-1} and above, [lact] increased exponentially as running speed increased, with average end-run concentrations increasing to 2.66±0.33, 7.83±0.94, and 33.76±2.39 mmol l^{-1} at 7, 12, and 15 m s^{-1}. $\dot{M}_{Lactate}$ were undetectable at running speeds below 7 m s^{-1} (approximately 70% $\dot{V}_{O_2}$max), averaged 8.0±0.5 mmol l^{-1} min^{-1} at 100% $\dot{V}_{O_2}$max, and 18.4±1.2 mmol l^{-1} min^{-1} at 115% of the speed required to elicit $\dot{V}_{O_2}$max. No significant correlations were found between $\dot{V}_{O_2}$max, end-run [lact], or $\dot{M}_{Lactate}$ and the running speed required to elicit $\dot{V}_{O_2}$max. Additionally, no significant correlation was found between the values of $\dot{V}_{O_2}$max and either $\dot{M}_{Lactate}$ or end-run [lact]. $\dot{V}_{O_2}$max and $\dot{M}_{Lactate}$ were identical on two sequential runs 1 h apart at a speed 1 m s^{-1} faster than that required to elicit $\dot{V}_{O_2}$max. However, compared to the first run, pre-run [lact] was significantly higher and end-run [lact] was lower for the second of the two runs. These results indicate that enhanced clearance of plasma lactate must have occurred during the submaximal and/or the initial maximal portion of the second run.

Key words Horses; exercise; lactate; $\dot{V}_{O_2}$max; aerobic metabolism; anaerobic metabolism.

INTRODUCTION

Many studies have investigated the relationship between changes in blood lactate concentration and running performance in horses.[3,14,19] Much effort has focused on the running speed that causes an initial increase in lactate concentration, the so-called "lactate threshold", because of its potential use in providing an index of aerobic capacity.[17,24] While this datum may be indicative of the exercise intensity at which lactate entry into the bloodstream exceeds lactate removal/oxidation, the interpretation of this information is controversial.[1,16,20,25]

Recent reports of the role of lactate in energy metabolism have demonstrated that lactate is not just a waste-product of anaerobic metabolism, but rather, can serve as a major oxidizable substrate for cardiac and skeletal muscle.[5,10] Thus, interpretation of lactate kinetics at increasing running speeds is confounded not only by increased rates of production, but potentially by increased rates of utilization as different muscle fiber types are recruited during exercise.[11,21–23] The lower lactate concentrations observed in trained athletes (both human and animal) during exercise at a particular intensity may represent an enhanced capacity to utilize lactate as an oxidizable substrate, rather than simply reduced production, as has been previously thought.[7,12]

The present study examines plasma lactate kinetics in the exercising horse during a protocol that includes running for 3 min at speeds eliciting $\dot{V}_{O_2}$max, and interprets the

changes in lactate kinetics during maximum aerobic exercise from this perspective.

METHODS AND MATERIALS

Six Thoroughbred geldings (5.8±0.8 (SD) years old, weighing 466±19 (SD) kg) were trained to run on a motorized treadmill (0% incline) until maximum rates of O_2 consumption ($\dot{V}_{O_2}max$) were reproducible (between run variation <2%). The horses wore a mask over their muzzles to capture expired gases for the measurement of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$). To measure $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$, air was drawn through the mask by a 25 hp turbine at flow rates of 8000 to 14000 l [STPD] min^{-1}. Prior to running on the treadmill, a 14 gauge ×15 cm catheter was introduced percutaneously into the left jugular vein of each horse. Heparinized blood samples (3 ml) drawn from these catheters were kept on ice (<1 h) until plasma could be separated by centrifugation at 1500 ×*G* for 5 min. The plasma was analyzed immediately for lactate concentration [lact] using an enzymatic procedure from Sigma Chemical Co. Plasma lactate accumulation rates ($\dot{M}_{Lactate}$, mmol l^{-1} min^{-1}) for a given exercise intensity were determined from the difference in lactate concentration and the time interval between two sequential blood samples collected at that running speed. The first of the two samples was typically collected after 1 min at a given exercise intensity, and the second 1.5–2 min later. Three distinct studies, outlined separately below, were performed during a 3 month period.

Determination of $\dot{V}_{O_2}max$

Horses exercised according to the following protocol: (1) a 3 min warm-up trot at 4 m s^{-1}; (2) standing quietly on the treadmill during the next 3 min while the gas collection mask was placed over the horse's muzzle; (3) 2 min at 4 m s^{-1}; (4) 2 min at 7 m s^{-1}; and (5) 3 min at one of either 10, 12, 13, 14, 15, 16, or 17 m s^{-1}. This protocol was repeated for each horse a minimum of 3 times for each of the speeds listed in step 5 above. Horses were run at speeds of 14 m s^{-1} and higher no more than 3 times a week. Concentrations of O_2 and CO_2 were continuously monitored in the expired gas line with O_2 (Ametek S-3A/II) and CO_2 (Beckman LB-2) analyzers. Rates of O_2 consumption and CO_2 production, corrected to STPD, were calculated using the N_2-dilution, CO_2-addition technique of Fedak et al.[9] Calibration gases (N_2 or CO_2) were metered into the mask via electronic mass flow meters (Matheson Gas Products Model 8210 Dyna-Blender). A schematic of the experimental set-up is presented in Fig. 1. ECG signals were collected from gel electrodes affixed to shaved areas of the neck and flank with cyanoacrylate cement, and were amplified and recorded on a strip chart recorder (Gould Inc. Brush 2400). The average heart rate was determined from these recordings during the last min of exercise at each running speed.

Time course of changes in plasma lactate concentration

For these trials, all horses followed the protocol described above with the exception that maximum running speed during the final 3 min was standardized at 14 m s^{-1}. Blood samples were drawn from the jugular catheter approximately every 30 s during the run at maximum speed, and after 1 and 2 min of walking at 1.5 m s^{-1} following the run. [Lact] were measured as described above.

Lactate concentrations during sequential runs

Each horse followed the same running protocol described above of 4 m s^{-1}, rest, 4 m s^{-1} and 7 m s^{-1}, then ran for 3 min at a maximum speed that was 1 m s^{-1} faster than the speed previously determined to be the minimum required to elicit $V_{O_2}max$ for that horse. Only 5 horses were able to complete this portion of the study. Blood samples were collected immediately prior to the warmup trot and over a timed interval during the final 90 s of running at the maximum

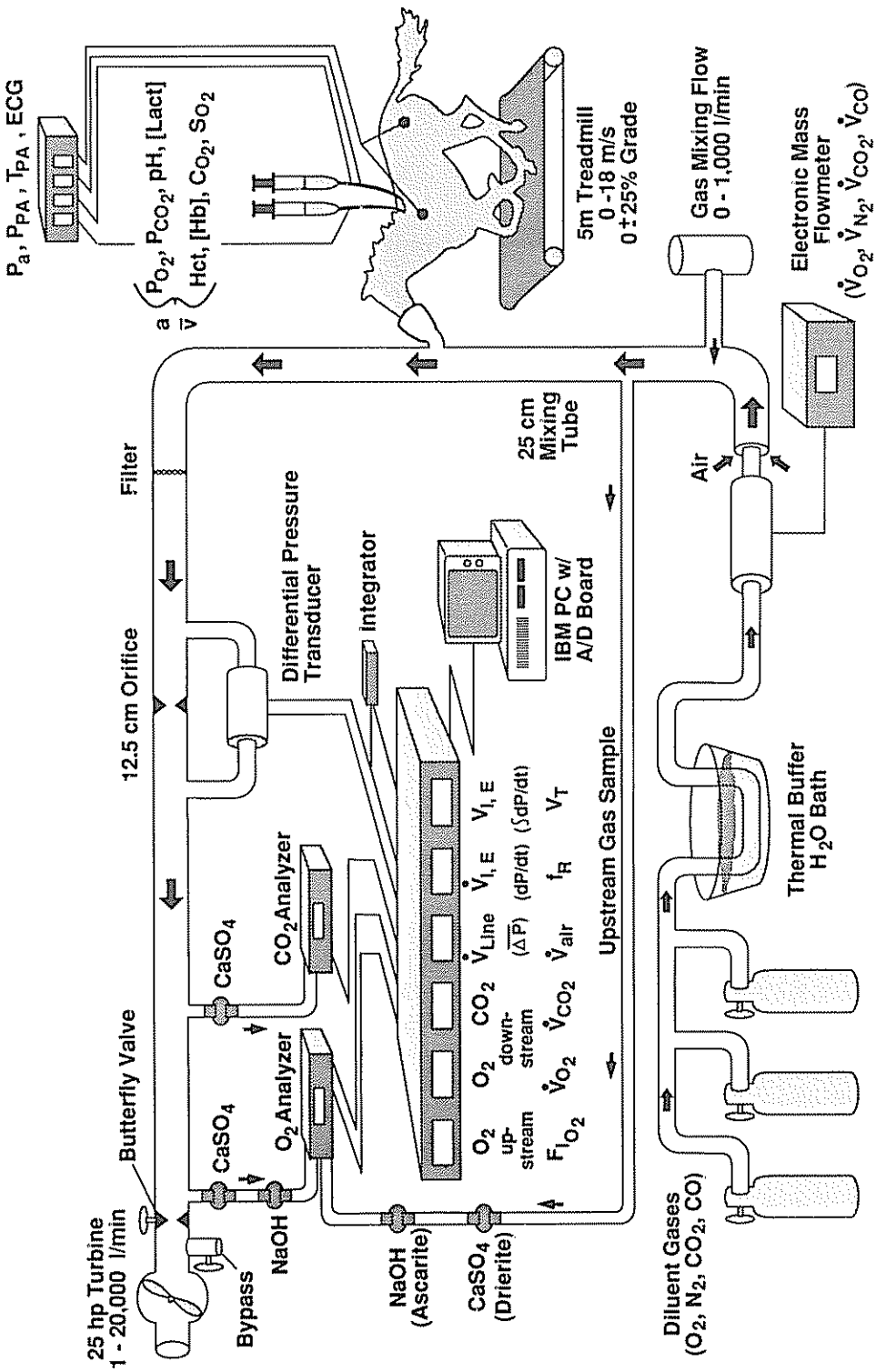

Fig. 1. A schematic of the experimental set-up utilized for these studies.

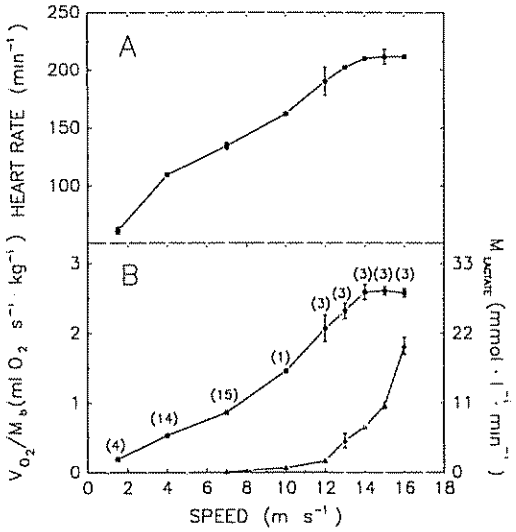

Fig. 2. (*a*) Heart rates at various exercise intensities in a single horse. Values are means ± SEM of multiple runs. The number of observations at each point is given in the bottom figure. (*b*) Mass specific oxygen consumption ($\dot{V}_{O_2}/M_b$) (circles) and plasma lactate accumulation rates (triangles) at various exercise intensities for the same horse. Values are means ± SEM.

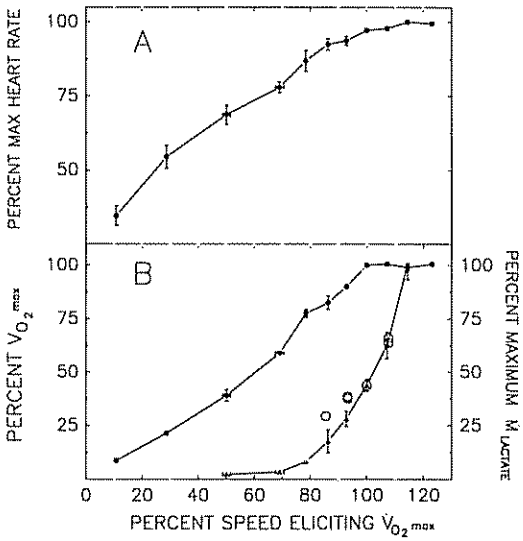

Fig. 3. (*a*) Heart rates standardized as percentage of maximum heart rate measured in each horse at exercise intensities standardized as the percentage of the speed required to elicit $\dot{V}_{O_2}$max in each of 6 horses; values are means ± SEM. (*b*) Rates of oxygen consumption (filled circles) and plasma lactate accumulation rates (triangles) standardized to their maximum values for each horse at running speeds standardized as above in (3*a*). Standardized plasma lactate accumulation rates (open circles) for 6 horses exercising at 14 m s^{-1}; values represent the average of 3 determinations for each horse during the final 1.5 min of each 3 min run.

speed. The horse walked on the treadmill (1.5 m s^{-1}) for 1 h at the conclusion of the run, and the sequence was repeated. $\dot{V}_{O_2}$, $\dot{M}_{Lactate}$, and [lact] immediately prior to the warm-up trot (pre-run) and after 3 min at the maximum speed (end-run) were determined.

Data analysis

Data reported are means ± SEM for these horses. Regression parameters were determined by least-squares with significance indicated for slopes different from zero. Where indicated, two-way ANOVA was utilized, and Tukey's HSD post-test was applied to comparisons for which $p<0.05$.

RESULTS

Determination of $\dot{V}_{O_2}max$

For all horses, $\dot{V}_{O_2}$ increased with running speed up to a speed, characteristic for each horse, above which no additional increase in $\dot{V}_{O_2}$ was observed (Fig. 2*b*, 3*b*). Mass specific $\dot{V}_{O_2}$max ($\dot{V}_{O_2}$max/M_b, where M_b is in kg), ranged from 2.34 to 2.69 ml O_2 s^{-1} kg^{-1} and was not correlated with the running speed required to elicit it ($r^2=0.008$, $p=0.86$) (Fig. 4*a*). The speed necessary to elicit $\dot{V}_{O_2}$max varied from 13 to 16 m s^{-1} among these horses. No accumulation of plasma lactate could be detected at running speeds below 7 m s^{-1}, but at higher speeds the accumulation rate increased exponentially as running speed increased (Fig. 2*b*, 3*b*). $\dot{M}_{Lactate}$ averaged 8.0±0.5 mmol l^{-1} min^{-1} at the minimum speed that elicited $\dot{V}_{O_2}$max (Fig. 3*b*). The maximum average $\dot{M}_{Lactate}$ (18.4±1.2 mmol l^{-1} min^{-1}) was measured at running speeds approximately 15% higher than those necessary to elicit $\dot{V}_{O_2}$max. Not all of the

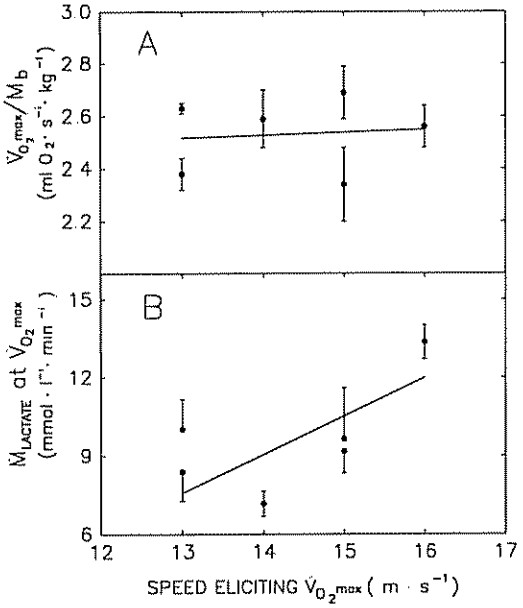

Fig. 4 (*a*) Average maximum mass-specific oxygen consumption ($\dot{V}_{O_2}max/M_b$) at the running speed required to elicit $\dot{V}_{O_2}max$ for 6 horses. The solid line indicates the least-squares regression for these data; regression equation: $\dot{V}_{O_2}max/M_b = 2.38 + (0.01 \times speed)$; $r^2 = 0.008$, $p = 0.86$. (*b*) Average plasma lactate accumulation rates at the running speed required to elicit $\dot{V}_{O_2}max/M_b$ for the same 6 horses. The solid line indicates the least-squares regression for these data; regression equation: Lactate accumulation rate $= -5.76 + (1.07 \times speed)$; $r^2 = 0.39$, $p = 0.19$.

horses were able to maintain running speeds greater than 115% of those required to elicit $\dot{V}_{O_2}max$ for and entire 3 min run. Therefore, only those runs for which the horses completed the 3 min maximum speed run are included. $\dot{M}_{Lactate}$ at the minimum speed eliciting $\dot{V}_{O_2}max$ was not significantly correlated with the speed required to elicit $\dot{V}_{O_2}max$ ($r^2 = 0.39$, $p = 0.19$) (Fig. 4*b*), nor with $\dot{V}_{O_2}max/M_b$ itself ($r^2 = 0.04$, $p = 0.70$). The relationship between running speed and average heart rate was similar to that observed for $\dot{V}_{O_2}$ (Fig. 2*a*, 3*a*). The average heart rates of the horses ranged from 73 to 211 min^{-1} for running speeds of 1.5 and 17 m s^{-1}, respectively.

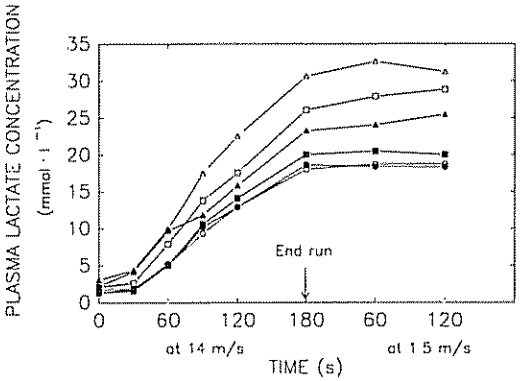

Fig. 5. Plasma lactate concentrations at various times during and immediately after running at 14 m s^{-1}. Each symbol represents observations from a different horse.

Time course of changes in lactate concentration

When [lact] were measured throughout the standardized exercise protocol with a maximum running speed of 14 m s^{-1}, similar profiles were observed for all horses (Fig. 5). For every horse, a lag of approximately 30 s occurred between the increase in treadmill speed and an increase in [lact]. Both the end-run [lact] and the rates of lactate accumulation differed among horses. End-run [lact] ranged from 18.0 to 30.6 mmol l^{-1}. For individual horses, $\dot{M}_{Lactate}$, determined at 30 s intervals (following the 30 s lag) were essentially linear during the run at maximum speed. Although $\dot{M}_{Lactate}$ differed for these horses running at 14 m s^{-1}, ranging from 7.4 to 12.1 mmol l^{-1} min^{-1}, when the running speeds were standardized to the percentage of the speed eliciting $\dot{V}_{O_2}max$ for each horse, the relationship between $\dot{M}_{Lactate}$ and percent of speed eliciting $\dot{V}_{O_2}max$ was similar to that observed in the first experiment (Fig. 3*b*).

Lactate concentrations during sequential runs

When plasma lactate accumulation measurements were made on sequential runs 1 h apart, no significant differences were detected in either $\dot{V}_{O_2}/M_b$ ($p = 0.87$) or in $\dot{M}_{Lactate}$

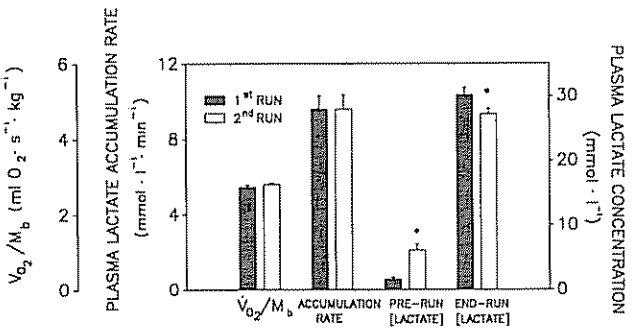

Fig 6 Oxygen consumption rates, plasma lactate concentrations, and plasma lactate accumulation rates during 2 sequential runs at 1 m s^{-1} faster than that required to elicit $\dot{V}_{O_2}$max. Horses walked (1.5 m s^{-1}) for 1 h between the first run (filled bar) and the second run (open bar). Values are means ± SEM from eleven paired runs using 6 different horses. * indicates significantly different from the corresponding pa, $p<0.01$

($p=0.91$) (Fig. 6). At the 0.05 α-level, these analyses had the power to detect 4% and 36% differences with 90% probability for $\dot{V}_{O_2}$max and $\dot{M}_{Lactate}$, respectively. $\dot{V}_{O_2}/M_b$ was 2.72±0.06 and 2.79±0.04 ml O_2 s^{-1} kg^{-1} for the first and second runs, respectively, and mean $\dot{M}_{Lactate}$ were 9.6±0.7 and 9.6±0.8 mmol l^{-1} min^{-1}. Pre-run [lact] were significantly higher for the second run than for the first run (6.1±1.0 vs 1.6±0.3 mmol l^{-1}; $p<0.0001$). Conversely, the end-run [lact] were significantly lower following the second run than the first run (27.2±0.9 vs 30.1±1.2 mmol l^{-1}; $p<0.01$).

DISCUSSION

Techniques to determine the maximum rate of O_2 consumption ($\dot{V}_{O_2}$max) have previously been described in detail.[18] To establish $\dot{V}_{O_2}$max for these horses, we used 3 criteria: (1) increases in running speed elicited no further increase in $\dot{V}_{O_2}$; (2) additional energy necessary to sustain these greater running speeds resulted in a net accumulation of plasma lactate; (3) r values ($\dot{V}_{CO_2}/\dot{V}_{O_2}$) exceeded 1.0. A plateau of $\dot{V}_{O_2}$ and heart rate is clearly shown for both a single horse (Fig. 2) and standardized for all the horses (Fig. 3). These data demonstrate nearly identical physiological response in all 6 horses when standardized, even though the $\dot{V}_{O_2}/M_b$ varied approximately 15% among horses.

Increased [lact] occur whenever production, coupled with movement into the bloodstream, exceeds removal by either storage (redistribution), oxidation or gluconeogenesis. Increased lactate production has been observed during exercise or through the recruitment of muscle fibers in which anaerobic glycolysis predominates for energy metabolism.[4,12] This study explores the relationship between O_2 consumption and plasma lactate accumulation, particularly at exercise intensities at or above those eliciting $\dot{V}_{O_2}$max, and for periods of time physiologically relevant to the racehorse.

No correlation was found between the value of $\dot{V}_{O_2}$max/M_b and the speed at which $\dot{V}_{O_2}$max is achieved (Fig. 4*a*). Therefore, it can be stated that a higher $\dot{V}_{O_2}$max/M_b does not translate directly to a faster horse. Indeed, this observation suggests that significant differences in efficiency (mechanical power output/metabolic power input) exist between horses. Furthermore, Fig. 4*b* indicates that at $\dot{V}_{O_2}$max, all horses have a similar rate of plasma lactate accumulation, approximately 8 mmol l^{-1}, again independent of the running speed at which $\dot{V}_{O_2}$max was elicited. This suggests that $\dot{M}_{Lactate}$ might be used as an index of $\dot{V}_{O_2}$max.

Numerous studies have reported an exponential increase in blood or plasma lactate concentration with increasing running speed similar to that described here.[8,17,24] Although other studies have investigated blood lactate concentration kinetics during exercise,[1,2,8] none have reported the delay in changes in [lact] following a change in exercise intensity observed in this study. Less than one-third of the observed 30 s time lag in onset of

plasma lactate accumulation following a step change in running speed can be explained by the time required for the treadmill to accelerate between speeds (< 10 s). The remainder of the time lag in concentration increase represents the time required to establish concentration gradients for diffusion of lactate from muscles into blood and for convective transport of the lactate to the sampling site. Knowledge of the percentage of the speed required to achieve $\dot{V}_{O_2}$max that is represented by a particular running speed is necessary to fully interpret the changes in [lact] and $\dot{M}_{Lactate}$ observed in this study.

Many reports suggest that repeated bouts of exercise are accompanied by progressive increases in [lact].[3,19] However, this study demonstrates that with 1 h of low intensity exercise (walking at 1.5 m s^{-1}) between bouts, [lact] at the end of the second supra-$\dot{V}_{O_2}$max run were *lower* than those observed at the end of the first (Fig. 6). In fact, [lact] were lower at all sample times during the final 1.5 min of the second supra-$\dot{V}_{O_2}$max run than for corresponding times of the first run. Despite the fact that [lact] after exercise have been shown to decrease more rapidly toward resting concentrations with continued low intensity exercise following a high intensity exercise bout,[6,15] the concentrations prior to the second run in this study remained significantly elevated compared with those observed prior to the first run. Thus, [lact] were higher prior to, and lower following, the second run at a supra-$\dot{V}_{O_2}$max speed. However, for both runs, $\dot{M}_{Lactate}$ during the portion of the run at $\dot{V}_{O_2}$max were identical. Therefore, enhanced lactate clearance must have occurred during the submaximal and/or initial maximal portion of the second run. Recent reports that aerobic training enhances lactate clearance capacity[7] and that lactate clearance rates are positively correlated with [lact][7,13] may explain these findings. Because of the elevated [lact] at the beginning of the second run, higher rates of lactate clearance at the lower speeds might have caused the total lactate accumulation during the combined submaximal and maximal run to be lower. A single observation from our laboratory suggests that there is less lactate accumulation during the initial 45 s of a second supra-$\dot{V}_{O_2}$max run, however, further experiments are required to verify and elucidate the mechanisms responsible for this finding.

Anaerobic metabolism in the exercising horse can only be accurately related to total energy metabolism by measuring the total turnover of lactate in the body during exercise, rather than just the net accumulation, as in this study. Measurement of total turnover rates requires the use of radiolabelled tracers or nuclear magnetic resonance spectroscopy to account for quantities of lactate that are produced and added to the whole-body pool in one part of the body while lactate is simultaneously oxidized and removed from the pool in another location, i.e., the "lactate shuttle".[4,7] Although these more complex experimental approaches are not presented here, simple measurements of lactate accumulation rates during exercise in horses do allow us to draw the following conclusions:

1) For horses that are moderately conditioned on a treadmill, no correlation exists between $\dot{V}_{O_2}$max/M_b and the speed that elicits $\dot{V}_{O_2}$max, suggesting that differences in their performance may be more related to variation in efficiency than strictly to aerobic power (Fig. 4*a*).

2) When a horse runs at the minimum speed that elicits $\dot{V}_{O_2}$max, lactate accumulates in the plasma at a rate of approximately 8 mmol l^{-1} min^{-1}, independent of speed and $\dot{V}_{O_2}$max/M_b for that horse (Fig. 4*b*).

3) $\dot{M}_{Lactate}$ correlate more highly with the percentage of running speed required to elicit $\dot{V}_{O_2}$max than with absolute running speed (Fig. 3*b*; Fig. 5).

4) During exercise at or near a work load that elicits $\dot{V}_{O_2}$max, plasma lactate accumulates at a steady rate after approximately 30 s following an increase in running speed; the rate of increase is directly correlated with the percentage of $\dot{V}_{O_2}$max at which the horse is working (Fig. 5). If a standardized exercise

protocol is followed, $\dot{M}_{Lactate}$ can be a useful estimator of aerobic capacity.

5) [Lact] are higher before, and lower after, a supra-$\dot{V}_{O_2}$max exercise protocol that follows a supra-$\dot{V}_{O_2}$max protocol 1 h earlier. Nevertheless, $\dot{V}_{O_2}$max/M_b and $\dot{M}_{Lactate}$ are identical during the supra-$\dot{V}_{O_2}$max portions of both runs (Fig. 6). These findings suggest that prior exercise results in increased rates of plasma lactate clearance during sub-$\dot{V}_{O_2}$ max exercise.

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REFERENCES

1 Astrand, P. and Rodahl, K. (1986). Physical performance. *In* Astrand, P. and Rodahl, K. (eds): *Textbook of Work Physiology. Physiological Bases of Exercise*, 3rd ed., McGraw-Hill Book Company, New York, pp. 295–353.

2 Babij, P., Matthews, S. M. and Rennie, M. J. (1983). Changes in blood ammonia, lactate, and amino acids in relation to workload during bicycle ergometer exercise in man. Eur. J. Appl. Physiol. 50, 405–411.

3 Bayly, W. M., Grant, B. D. and Pearson, R. C. (1987). Lactate concentrations in Thoroughbred horses following maximal exercise under field conditions. *In* Gillespie, J. R. and Robinson, N. E. (eds.): *Equine Exercise Physiology 2*, ICEEP Publications, Davis, CA, pp. 426–437.

4 Brooks, G. A. and Fahey, T. D. (1985). Metabolic response to exercise. *In* Brooks, G. A. and Fahey, T. D. (eds.): *Exercise Physiology. Human Bioenergetics and Its Applications*, Macmillan Publishing Co., New York, pp. 189–220.

5 Connett, R. J., Gayeski, T. E. J. and Honig, C. R. (1984). Lactate accumulation in fully aerobic, working, dog gracilis muscle. Am. J. Physiol. 246, H120–H128.

6 Dodd, S., Powers, S. K., Callender, T. and Brooks, C. (1984). Blood lactate disappearance at various intensities of recovery exercise. J. Appl. Physiol. 57, 1462–1465.

7 Donovan, C. M. and Brooks, G. A. (1983). Endurance training affects lactate clearance, not lactate production. Am. J. Physiol. 244, E83–E92.

8 Essén-Gustavsson, B. and Valberg, S. (1987). Blood and muscle ammonia concentrations in horses during treadmill work and after racing. *In* Gillespie, J. R. and Robinson, N. E. (eds.): *Equine Exercise Physiology 2*, ICEEP Publications, Davis, CA, pp. 456–463.

9 Fedak, M. A., Rome, L. and Seeherman, H. J. (1981). One-step N_2-dilution technique for calibrating open-circuit $\dot{V}_{O_2}$ measuring systems. J. Appl. Physiol.: Resp. Environ. Exerc. Physiol. 51, 772–776.

10 Hochachka, P. W., Rungiman, W. B. and Baudinette, R. V. (1985). Why exercising tammar wallabies turn over lactate rapidly. Implications for models of mammalian exercise metabolism. Mol. Physiol. 7, 17–28.

11 Hodgson, D. R., Rose, R. J. and Allen, J. R. (1983). Muscle glycogen depletion and repletion patterns in horses performing various distances of endurance exercise. *In* Snow, D. H., Persson, S. G. B. and Rose, R. J. (eds.): *Equine Exercise Physiology*, Granta Editions, Cambridge, pp. 229–236.

12 Katz, A. and Sahlin, K. (1988). Regulation of lactic acid production during exercise. J. Appl. Physiol. 65, 509–518.

13 Katz, J., Okajima, F., Chenoweth, M. and Dunn, A. (1981). The determination of lactate turnover *in vitro* with ^{3}H- and ^{14}C-labelled lactate. Biochem. J. 194, 513–524.

14 Kubo, K., Takagi, S., Murakami, M. and Kai, M. (1984). Heart rate and blood lactate concentration of horses during maximal work. Bull. Equine Res. Inst. 21, 39–45.

15 Marlin, D. J., Harris, R. C., Harman, J. C. and Snow, D. H. (1987). Influence of post-exercise activity on rates of muscle and blood lactate disappearance in the Thoroughbred horse. *In* Gillespie, J. R. and Robinson, N. E. (eds.): *Equine Exercise Physiology 2*, ICEEP Publications, Davis, CA, pp. 321–331.

16 Morton, R. H. (1989). Detection of a lactate threshold during incremental exercise? J. Appl. Physiol. 67, 885–888.

17 Persson, S. G. B. (1983). Evaluation of exercise tolerance and fitness in the performance horse. *In* Snow, D. H., Persson, S. G. B. and Rose, R. J. (eds.): *Equine Exercise Physiology*, Granta Editions, Cambridge, pp. 441–457.

18 Seeherman, H. J., Taylor, C. R., Maloiy, G. M. O. and Armstrong, R. B. (1981). Design of the mammalian respiratory system. II. Measuring maximum aerobic capacity. Resp. Physiol. 44, 11–23.

19 Snow, D. H. and MacKenzie, G. (1977). Some metabolic effects of maximal exercise in the horse and adaptations with training. Equine Vet. J. 9, 134–140.

20 Stegmann, H. and Kindermann, W. (1982). Comparison of prolonged exercise tests at the individual

anaerobic threshold and the fixed anaerobic threshold of 4 mmol l^{-1} lactate. Int J. Sports Med 3, 105–112

21 Sullivan, I. and Armstrong, R. (1978) Rat locomotory muscle fiber activity during trotting and galloping J Appl Physiol. 44, 358–363.

22 Valberg, S. (1986) Glycogen depletion patterns in the muscle of Standardbred trotters after exercise of varying intensity and duration. Equine Vet. J. 18, 479–484

23 Valberg, S. and Essén-Gustavsson, B. (1987) Metabolic response to racing determined in pools of type I, II A, and II B fibers *In* Gillespie, J. R. and Robinson, N. E. (eds.): *Equine Exercise Physiology 2*, ICEEP Publications, Davis, CA, pp. 290–301.

24 Wilson, R. G., Islere, R. B. and Thornton, J. R. (1983) Heart rate, lactic acid production and speed during a standardized exercise test in Standardbred horses. *In* Snow. D. H., Persson, S. G. B. and Rose, R. J. (eds.): *Equine Exercise Physiology*, Granta Editions, Cambridge, pp. 487–496.

25 Yeh, M. P., Gardner, R. M., Adams, T. D., Yanowitz, F. G. and Crapo, P. O. (1983). "Anaerobic threshold": Problems of determination and validation J. Appl. Physiol.: Resp. Environ. Exerc. Physiol. 55, 1178–1186

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Rates of Blood Lactate Disappearance Following Exercise of Different Intensities

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ABSTRACT. Lactate was analysed in whole blood and plasma following 2 min treadmill exercise on separate occasions at 6, 7, 8, 9, 10, 11 or 12 m s^{-1} on a 5° incline. Peak concentrations of lactate in plasma were found to occur immediately post-exercise (0 min recovery) when the peak concentration was less than 20 mmol l^{-1} and at 5 min recovery between 20–46 mmol l^{-1}. In whole blood, peak lactate concentrations occurred immediately post-exercise for concentrations less than 10 mmol l^{-1}. Between 15 and 30 mmol l^{-1}, peaks occurred at both 5 and 10 min recovery. Mean blood or plasma lactate disappearance rates (mmol l^{-1} h^{-1}) did not change significantly with increasing speed. Rates of disappearance ranged from 25.1–63.0 mmol l^{-1} h^{-1} for plasma and from 16.8–33.4 mmol l^{-1} h^{-1} for whole blood.

Key words. Horses; exercise; blood; lactate kinetics

INTRODUCTION

The kinetics of blood lactate appearance and disappearance following maximal field and treadmill exercise in the Thoroughbred horse have been described previously.[10,14] Following field gallops of either 800 or 2 000 m or treadmill gallops of 1 400 m at 12 m s^{-1} (5° incline), peak post-exercise blood lactate contents were found to occur between 5 and 10 min into recovery. Blood lactate appearance and disappearance could be described by a bi-exponential equation previously used to describe postexercise lactate kinetics in man.[7,8]

In both of the previous studies, lactate kinetics following exercise were examined over a relatively narrow range of initial lactate concentrations. The present investigation was, therefore, undertaken to investigate lactate kinetics over a much wider range of peak concentrations.

MATERIALS AND METHODS

Animals. Six trained Thoroughbred horses (FR—5 yo; HR—6 yo; JW—13 yo; MR—4 yo; TB—5 yo; LB—4 yo) were used in this study.

Exercise protocol. Each horse performed 7 experimental treadmill sessions, each separated by at least 3 days. Each experimental session consisted of a warm-up period during which the horses were walked for 15 min at 1.6 m s^{-1}, followed by a canter for 2 min at 6 m s^{-1} and a further 5 min walk at 1.6 m s^{-1}. After the warm-up period the horses performed a 2 min test-exercise at a speed of 6, 7, 8, 9, 10, 11 or 12 m s^{-1} (see Fig. 1). Only one speed was used per experimental session and the order of the sessions was randomised. The treadmill was set at 5° at all times during the warm up and exercise periods and at 0° during the recovery period. Environmental conditions were maintained between 18–20°C and 60–70% relative humidity.

Sampling. Blood samples were collected from an indwelling catheter (Becton–Dickinson, 14 g with 17 g×20 cm inner needle) located in the left or right jugular vein and attached to a 100 cm extension line (Lectrofelx, PVC, Vygon, UK, 2 ml capacity). Pa-