

- Rowell, L. B. (1974). Human cardiovascular adjustments to exercise and thermal stress. *Physiol. Rev.* **54**, 75–159.
- Sanders, T. M., Werner, R. A. and Bloor, C. M. (1976). Visceral blood flow distribution during exercise in conscious dogs. *J. Appl. Physiol.* **40**, 927–931.
- Sanders, M., Rasmussen, S., Cooper, D. and Bloor, C. (1976). Renal and intrarenal blood flow distribution in swine during severe exercise. *J. Appl. Physiol.* **40**, 932–935.
- Steel, R. G. D. and Torrie, J. H. (1960). *Principles and Procedures of Statistics*. McGraw-Hill Book Co., NY.
- Van Citters, R. L. and Franklin, D. L. (1969). Cardiovascular performance of Alaska sled dogs during exercise. *Circ. Res.* **24**, 33–42.
- Vatner, S. F., Higgins, C. B. and Franklin, D. L. (1972). Regional circulatory adjustments to moderate and severe chronic anemia in conscious dogs at rest and during exercise. *Circ. Res.*, **30**, 731–740.
- Vatner, S. F., Higgins, C. B., Millard, R. W. and Franklin, D. (1974). Role of spleen in the peripheral vascular response to severe exercise in untethered dogs. *Cardiovasc. Res.* **8**, 276–282.
- Wade, O. L. and Bishop, J. M. (1962). The distribution of cardiac output in normal subjects during exercise. *In: Cardiac Output and Regional Blood Flow*. Blackwell Scientific Co., Oxford.

# Respiratory Gas Exchange Kinetics In Transition from Rest or Prior Exercise In Ponies

S. K. POWERS<sup>1</sup>, R. E. BEADLE, J. LAWLER, and D. THOMPSON  
School of Veterinary Medicine and School of HPERD, Louisiana State University, Baton Rouge, LA 70803, USA

## Summary

*The purposes of these experiments were to examine gas exchange kinetics in the pony ( $n = 5$ ) during the transition from rest to exercise and to compare the rate of gas exchange adaptation during the transition from a low work rate to a moderate work load. The treadmill work rates studied were 1) rest to 70 m/min, 7% grade and 2) rest to steady state exercise at 40 m/min, 7% grade followed by an abrupt increase in treadmill speed to 70 m/min 7% grade. The kinetic response of expired ventilation, expired carbon dioxide, and heart rate was unaffected by exercise intensity or whether the transition was made from rest or prior exercise. Further, with similar metabolic increments, the rate of oxygen uptake ( $\dot{V}O_2$ ) adaptation from rest to exercise was not significantly different from the  $\dot{V}O_2$  time course during the transition from one work rate to a higher work rate. In contrast, the  $\dot{V}O_2$  half times were significantly greater during the transition from rest to 40 m/min, 7% grade when compared to the transition from rest to 70 m/min, 7% grade. It is hypothesized that the half-time of  $\dot{V}O_2$  in the pony during light to moderate exercise is principally influenced by the cardiodynamic phase of pulmonary gas exchange and thus does not reflect oxygen uptake by the muscle. Hence, the finding that  $\dot{V}O_2$  kinetics differs as a function of work rate should not be interpreted as a direct indication of differences in the rate of muscle metabolism.*

*Index terms: Ventilation, oxygen uptake.*

## Introduction

In humans, it is generally agreed that in the transition from rest to submaximal exercise, oxygen uptake ( $\dot{V}O_2$ ) and carbon dioxide output ( $\dot{V}CO_2$ ) measured via pulmonary gas exchange increase toward steady-state in a monoexponential fashion (Henry, 1951; Linnarsson, 1974; Whipp, 1971). Further, there is general agreement that the kinetics of  $\dot{V}O_2$  and  $\dot{V}CO_2$  adaptation are characterized by half times of approximately 30 and 45 sec, respectively. However, controversy exists concerning the rate of  $\dot{V}O_2$  and  $\dot{V}CO_2$  adaptation in the transition from one work rate to another higher work rate. Some investigators have reported a faster adaptation of both  $\dot{V}O_2$  and  $\dot{V}CO_2$  when a given work

rate was achieved from prior exercise as opposed to rest (di Prampero *et al.*, 1970; Davies *et al.*, 1972), while others have found no change (Diamond *et al.*, 1977), and still others report delayed kinetics (Hughson and Morrissey, 1982). Additional research to resolve this conflict is warranted.

Recent interest in the pony as a model to study ventilatory and metabolic adaptations to exercise stress has produced several papers (Bisgard *et al.*, 1978; Forster *et al.*, 1984; Pan *et al.*, 1983; 1984). Forster *et al.* (1984) have suggested that the rate of change in  $\dot{V}O_2$  from rest to steady state exercise in the pony differs from man and is clearly not best represented by a simple monoexponential function. Unfortunately, these investigators did not support their claim using a mathematical curve fitting technique. To date, little is known about the kinetics of respiratory gas exchange in horses and ponies at the onset of exercise. An understanding of the phenomenology of gas exchange kinetics has important implications in the study of control factors of oxygen transport and utilization. Therefore, the primary purpose of this study was to examine gas exchange kinetics in the pony during the transition from rest to exercise and from a low work rate to a moderate work load. A secondary purpose of these experiments was to compare the rate of gas exchange during the transition from rest to light exercise and from rest to moderate exercise.

### *Materials and Methods*

*Experimental design and animals.* Five healthy Welsh-Shetland mixed breed ponies, weighing  $191 \pm 32$  kg (mean  $\pm$  SD), were maintained at pasture for 32 weeks before experimentation with free access to hay and water. To aid in reduction of psychophysiological influences associated with the experimental protocol, the animals were exposed to the laboratory environment approximately twice weekly for 8 weeks prior to any data collection. Laboratory exposure included handling by laboratory personnel and all facets of the experimental protocol.

To determine the temporal pattern of  $\dot{V}O_2$ ,  $\dot{V}CO_2$ , and  $\dot{V}_E$  during exercise, each animal was studied on two occasions, separated by 2–5 days. Gas exchange and ventilatory measurements were made at rest and every 15 sec during treadmill exercise. The workloads selected for study were: 1) rest to steady state exercise at 70 m/min (7% grade) and 2) rest to steady state exercise at 40 m/min (7% grade) followed by an abrupt increase in treadmill speed to 70 m/min (7% grade). Animals exercised for a total of 4 min during test 1, i.e. rest to 70 m/min and a total of 8 min during test 2, i.e. 4 min at each load. These work loads were chosen because they represent light and moderate work rates and are below the anaerobic threshold as determined by arterial pH ( $pH_a$ ). Further, the step increment used in these experiments was selected so that the increase in steady state  $\dot{V}O_2$  from rest to 40 m/min was comparable to the change in steady state  $\dot{V}O_2$  when going from 40 m/min to 70 m/min, i.e.  $\dot{V}O_2$  increase of approximately 1.0–1.5 l/min. Order of treatment was randomly selected and animals were tested at the same time of day during each experiment. All studies were conducted at least 3.5–4.0 h after eating and performed under uniform environmental conditions: temperature = 19–21°C; relative humidity = 53–64%; barometric pressure = 761–766 torr.

*Data collection.* Immediately before each experiment, bipolar surface electrodes were attached to the pony's chest by an elastic belt and connected to a cardiometer (model HR/6, EQB, Unionville, PA) to measure heart rate (HR) during the experiment.

A mask with attached non-rebreathing valve was then placed on the pony's muzzle to allow measurement of ventilation and gas exchange during the course of the experiments. Each exercise was preceded by a 15 min rest period with an investigator stationed on each side of the animal's head to position the animal with the halter, if needed, during work. Metal walls on the sides of the treadmill restricted the animal's view thus reducing outside disturbing influences on respiratory gas exchange.

Following a 13 min rest period, measurements of  $\dot{V}_E$ , breathing frequency ( $f$ ), HR, and pulmonary gas exchange were made over a 2 min period. After collection of the final gas sample from the resting animal, the treadmill was started at a preselected speed and elevation. Measurements of  $\dot{V}_E$ ,  $f$ , HR, and gas exchange were made every 15 sec throughout work and recovery using open-circuit spirometry.

*Measurement of gas exchange.* Inspired ventilation was measured by a dry gas meter (Ram-9200, Rayfield Electronics, Chicago, IL) fitted with a potentiometer. Expired ventilation was channeled from a low resistance non-rebreathing valve through 85 cm length of 6.25 cm diameter tubing into a 9.2 l mixing chamber. Dead space of the mask and attached breathing valve was approximately 350 ml. Resistance on the inspired side of the valve (including tubing and dry gas meter) at a flow of 7 l/sec was 1.1 cm H<sub>2</sub>O/l/sec while resistance on the expired side of the valve at flows of 7 l/sec was 0.4 cm H<sub>2</sub>O/l/sec.

Gas was sampled from the exit port of the mixing chamber at a rate of 300 ml/min by an Applied Electrochemistry S-3A oxygen analyzer and an Applied Electrochemistry CD-3 carbon dioxide analyzer (Pittsburgh, PA). Electrical signals from the gas analyzers and dry gas meter underwent analog to digital conversion and were sent to a Rockwell Aim-65 microcomputer for processing which provided a hard copy of all calculated variables, i.e. oxygen uptake, carbon dioxide output, etc. When performing calculations of gas exchange variables, it was necessary to introduce a time delay to account for the washout characteristics of the mixing chamber and the response time of the gas analyzers. This technique has been shown to provide accurate measures of gas exchange in both humans and large animals (Powers, 1987).

*Statistical analysis.* To characterize the kinetic behavior of  $\dot{V}O_2$ ,  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR precisely in each condition, the response for each animal was fit by a least squares gradient algorithm (Daniel and Wood, 1980) to four competing functions:

$$f(x) = a(1 - e^{-k_1 t}) - (ae^{-k_2 t}) \quad (1)$$

$$f(x) = a(1 - e^{-k_1 t}) \quad (2)$$

$$f(x) = a(1 - e^{-k_1 t}) + b(1 - e^{-k_2 t}) \quad (3)$$

$$f(x) = a(1 - e^{-k_1 t}) + b(1 - e^{-k_2 t}) - (be^{-k_3 t}) \quad (4)$$

where  $f(x)$  may be the increase in  $\dot{V}O_2$ ,  $\dot{V}CO_2$ , HR, or  $\dot{V}_E$  above resting level at time  $t$ ;  $a$  and  $b$  are computed parameters that represent changes in amplitude;  $k_1$ ,  $k_2$ , and  $k_3$  represent rate constants; and  $t$  is time expressed in sec.

The kinetic parameter chosen for comparison was the half-time required for each measured variable to reach steady state. Half-times were computed for each of the following transitions: 1) rest to 40 m/min, 2) rest to 70 m/min, and 3) 40 m/min to 70 m/min. Analysis of variance techniques were used to compare the half times between tests, and a Newman-Keuls test used to determine significant differences with the critical  $P$  value set at 0.05 (Hayes, 1973).

## Results

Table 1 contains the individual values for proportion of total variance accounted for by each model and sums of squares for residuals for the model fit during the rest to 70 m/min experiment. This experiment was chosen to be used as an example since adequacy of model fits were comparable in each of the experimental conditions.

Models 1 and 2 yielded the lower ( $P < 0.05$ ) residual sums of squares for  $\dot{V}O_2$ ,  $\dot{V}CO_2$ , and HR when compared to models 3 and 4 (Table 1). In contrast, no significant difference ( $P > 0.05$ ) existed between the residual sums of squares for models 1 and 2 for these variables. Further, models 1, 2, and 4 resulted in similar sums of squares ( $P > 0.05$ ) for  $\dot{V}_E$ ; however, models 1, 2, and 4 each had lower ( $P < 0.05$ ) sums of squares than model 3. Thus, in general, these data suggest that a monoexponential function (model 2) provides an adequate fit for ventilatory and gas exchange data during non-steady state exercise in the pony. Support for the notion that model 2 provides adequate goodness-of-fit can be visualized in Fig. 1–4. Animal 2 was chosen as a representative example because the sums of squares for this animal were similar to or slightly greater than the mean sums of squares ( $n = 5$ ) for the 4 physiological parameters.

Figures 5–8 present the mean changes in  $\dot{V}O_2$ ,  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR, respectively, during the 3 exercise conditions. As the imposed square-wave forcing function of work rate was chosen below each animal's anaerobic threshold, the ensuing steady states of  $\dot{V}O_2$ ,  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR were reached within the 4 min duration of exercise. The characteristics of the corresponding dynamic responses, however, differed between  $\dot{V}O_2$ ,  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR. For example, both  $\dot{V}O_2$  and HR increased abruptly upon exercise, followed by a slower rise to a zenith within 45–60 sec and then decreased slightly to reach a steady state by 180 sec. Similarly,  $\dot{V}CO_2$  and  $\dot{V}_E$  increased quickly following the commencement of work, but then developed exponentially to reach steady state within 180 sec.

Half-times for  $\dot{V}O_2$ ,  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR for all experimental conditions are contained in Table 2. No significant differences ( $P > 0.05$ ) in  $\dot{V}_E$  or HR half-times existed between condition. Further, although the half-times for the adjustment of  $\dot{V}CO_2$  during the transition from rest to 70 m/min tended to be higher than those recorded for the rest to 40 m/min and work-to-work treatment, the differences were not significant.

TABLE 1. Non-linear least squares summary for justification of goodness-of-fit of 4 models used to determine oxygen uptake ( $\dot{V}O_2$ ) kinetics, respiratory carbon dioxide ( $\dot{V}CO_2$ ) kinetics, expired ventilation ( $\dot{V}_E$ ) kinetics and heart rate (HR) kinetics during the transition from rest to constant load exercise (70 m/min-7% grade).

	Model 1		Model 2		Model 3		Model 4	
	SSR	PTV	SSR	PTV	SSR	PTV	SSR	PTV
$\dot{V}O_2$	0.93 ± 0.19	991 ± 003	0.96 ± 0.18	989 ± 003	1.13 ± 0.17	990 ± 003	1.12 ± 0.30	991 ± 003
$\dot{V}CO_2$	0.77 ± 0.14	993 ± 003	0.76 ± 0.13	992 ± 003	1.24 ± 0.23	990 ± 003	1.23 ± 0.23	990 ± 003
$\dot{V}_E$	2504 ± 746	994 ± 003	2502 ± 747	994 ± 003	4189 ± 512	989 ± 003	1965 ± 532	993 ± 002
HR	353 ± 115	993 ± 003	351 ± 115	991 ± 003	573 ± 278	991 ± 003	1467 ± 965	977 ± 012

Values are means ± SEM

SSR—Sum of squares for residuals

PTV—Proportion of total variance accounted for by the model where PTV = sum of squares regression/sum of squares total

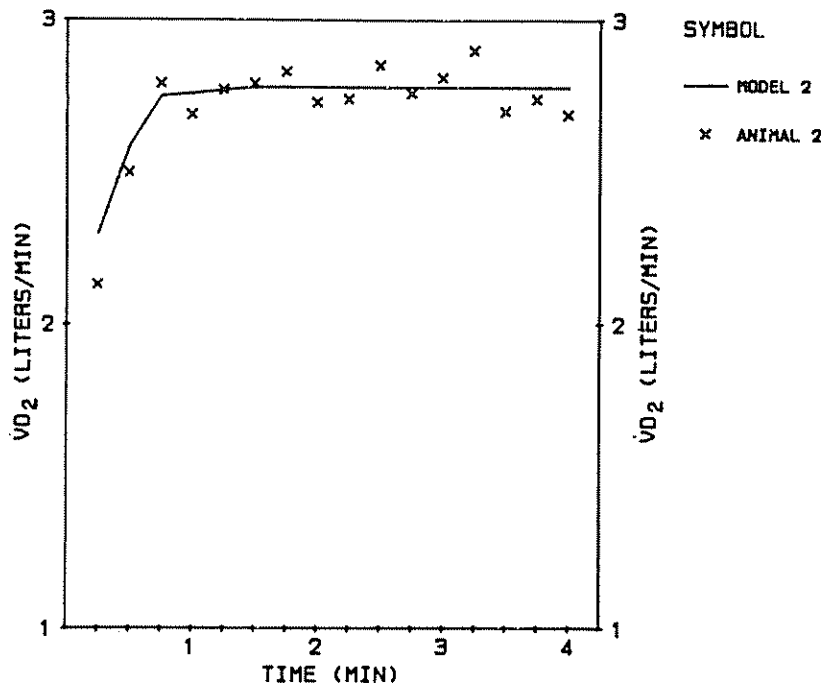


FIGURE 1 An illustration of goodness-of-fit of model 2 to oxygen uptake ( $\dot{V}O_2$ ) data during the transition from rest to exercise. The solid line indicates the model predicted pattern of  $\dot{V}O_2$  during exercise whereas (x) represents individual measurements for animal #2. Exercise work rate was 70 m/min at 7% grade.

( $P > 0.05$ ). Additionally, no significant difference ( $P > 0.05$ ) existed between the work-to-work transition  $\dot{V}CO_2$  half time and the rest to 40 m/min  $\dot{V}CO_2$  half time.

The half time for  $\dot{V}O_2$  in the transition from rest to 70 m/min was significantly longer ( $P < 0.05$ ) than the calculated half times for the two other experimental conditions. In contrast, no significant difference ( $P > 0.05$ ) existed between  $\dot{V}O_2$  half times for the rest to 40-m/min and work-to-work treatments.

### Discussion

*Critique of models.* Model comparisons were made by contrasting the residual sums of squares, which provides an index of the error between the actual data points and the calculated mathematical function. Although model 1 yielded the lowest residual sum of squares for  $\dot{V}O_2$  during the transition from rest to work when compared to models 2–4, the goodness-of-fit of model 1 to the data was not statistically superior ( $P > 0.05$ ) to model 2. Therefore, model 2 would seem to be the function of choice to describe  $\dot{V}O_2$  kinetics in the pony based on the predilection towards accepting the simplest explanation for observed phenomenon. Similarly, models 1 and 2 resulted in the lower residual sums of squares when compared to models 3 and 4 for  $\dot{V}CO_2$  and HR data. No significant difference ( $P > 0.05$ ) existed between models 1 and 2 in the goodness-of-fit to either  $\dot{V}CO_2$  or HR data. Further, models 1, 2, and 4 were found superior to

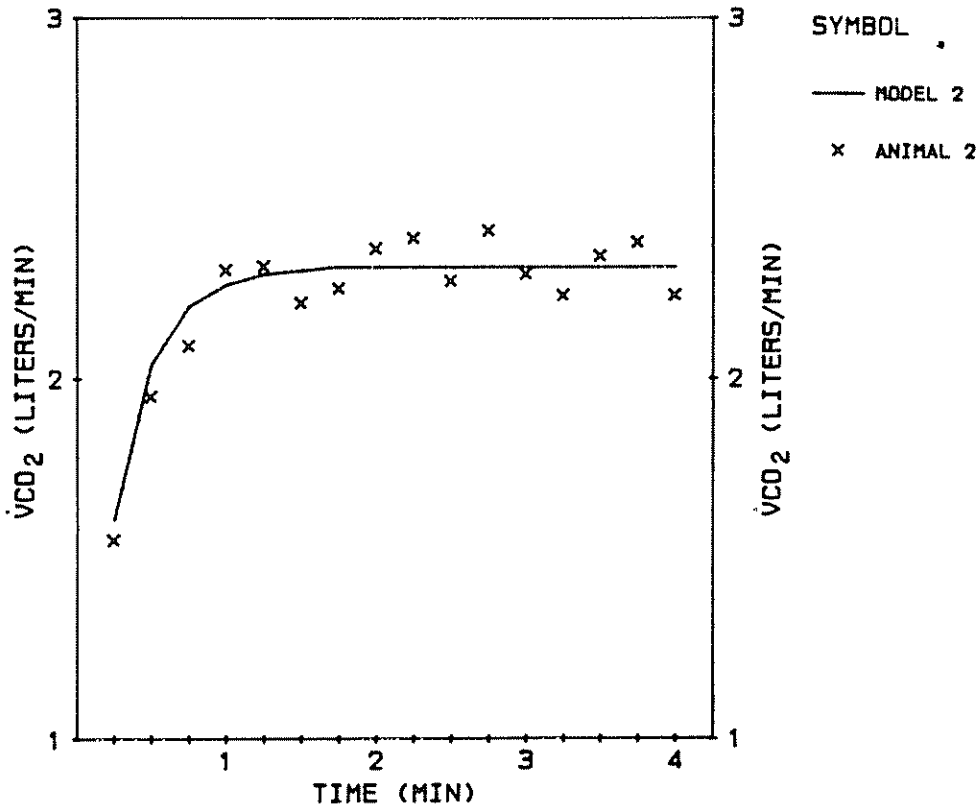


FIGURE 2. An illustration of goodness-of-fit of model 2 to carbon dioxide output ( $\dot{V}CO_2$ ) data during the transition from rest to exercise. The solid line indicates the model predicted pattern of  $\dot{V}CO_2$  during exercise whereas (x) represents individual measurements for animal #2. Exercise work rate was 70 m/min at 7% grade.

model 3 for  $\dot{V}_E$  data; however, no significant difference ( $P > 0.05$ ) existed between the sums of squares for models 1, 2, and 4 for  $\dot{V}_E$  data. Again, the monoexponential function (model 2) would appear to be the model of choice for simplicity for  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR.

The finding that gas exchange kinetics can be adequately described by a monoexponential function is in opposition to the suggestion by Forster *et al.* (1984) that  $\dot{V}O_2$  kinetics at the onset of exercise in the pony is not best represented by a monoexponential model. However, two points of interpretive caution need to be raised. First, the work rates used by Forster *et al.* (1984) to study gas exchange in ponies were higher than those employed in the present experiments. Therefore, the possibility exists that high work rates may elicit a slightly different  $\dot{V}O_2$  pattern than that observed during the light work rates used in the present experiments. Second, the inability to measure gas exchange on a breath-by-breath basis limits resolution and thus may allow a rapid "early" phase of gas exchange at the onset of exercise to go unnoticed. Whipp *et al.* (1982) have argued that an early phase of  $\dot{V}O_2$ ,  $\dot{V}CO_2$ , and  $\dot{V}_E$  at the onset of work is clearly distinguishable from the subsequent pattern of gas exchange when examined

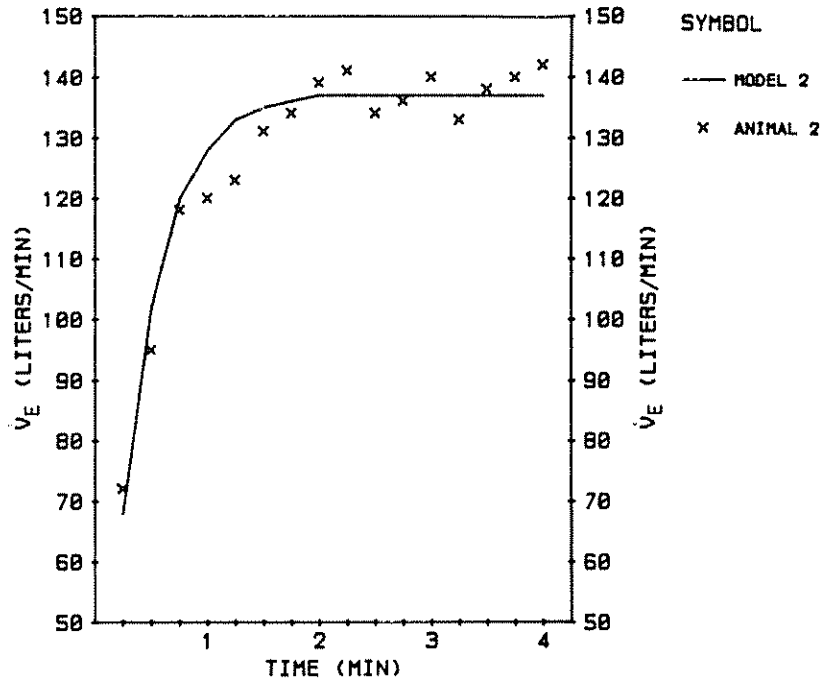


FIGURE 3. An illustration of goodness-of-fit of model 2 to ventilatory data ( $\dot{V}_E$ ) during the transition from rest to exercise. The solid line indicates the model predicted pattern of  $\dot{V}_E$  during the rest-to-work transition whereas (x) represents individual measurements for animal #2. Exercise work rate was 70 m/min at 7% grade.

breath-by-breath. To date, breath-by-breath measurements have not been performed during exercise in ponies. This presents an interesting challenge for future work.

*VO<sub>2</sub> kinetics.* Oxygen uptake across the alveolocapillary membrane is dictated in large part by the amount of reduced hemoglobin flowing through the lungs and by its degree of reduction (Whipp *et al.*, 1982). Therefore, following an abrupt increase in work rate, a change in venous oxygen content and oxygen partial pressure from the contracting muscles will not influence pulmonary gas exchange for the period of transit delay to the lungs. Thus, the initial increase in  $\dot{V}O_2$  observed during the rest-to-work or work-to-work transition probably reflects an increased pulmonary blood flow resulting from the exercise induced increase in cardiac output (Auchincloss *et al.*, 1966; Linnarsson, 1974; Wasserman *et al.*, 1974). Whipp *et al.* (1982) have called this first phase of gas exchange "cardiodynamic." However, when mixed venous oxygen levels subsequently change, a further increase in  $\dot{V}O_2$  would be expected (Weissman *et al.*, 1982; Whipp and Mahler, 1980) and thus may account for the "second" portion of the rise in  $\dot{V}O_2$  toward steady state. Hence, it seems likely that the kinetics of pulmonary oxygen uptake at the onset of muscular exercise cannot be directly related to events occurring in the working muscle.

The present data demonstrate that the rate of adaptation of  $\dot{V}O_2$  in the transition from rest-to-work and from work-to-work are not significantly different ( $P > 0.05$ ), provided

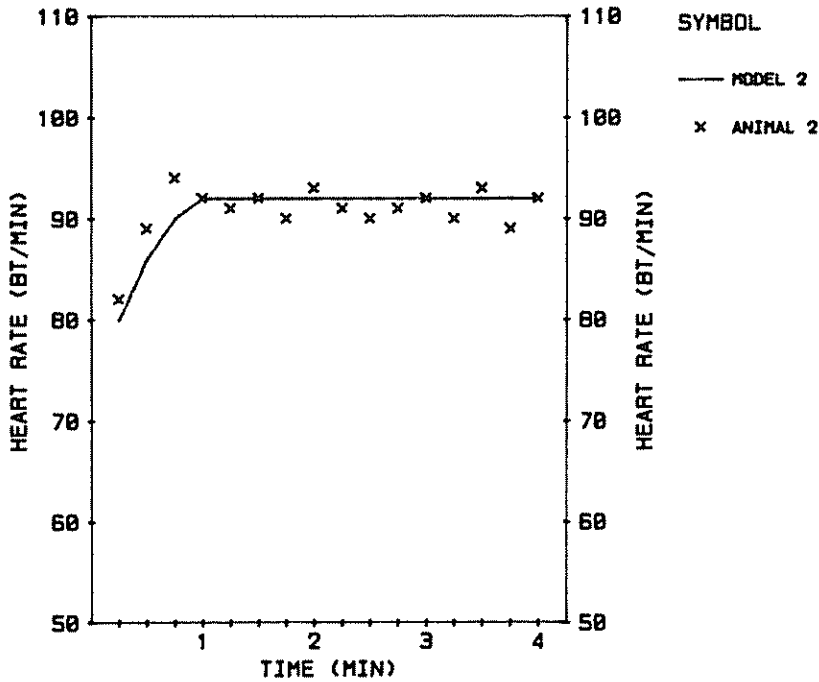


FIGURE 4 An illustration of goodness-of-fit of model 2 to heart rate (HR) data during the transition from rest to exercise. The solid line indicates the model predicted pattern of HR during exercise whereas (x) represents individual measurements for animal #2. Exercise work rate was 70 m/min at 7% grade.

that the metabolic increments are similar. This finding is in agreement with work using human subjects by Diamond *et al.* (1977) but disagrees with published data by di Prampero *et al.* (1970) and Davies *et al.* (1972). The reasons for the apparent discrepancy are not completely clear. However, di Prampero *et al.* (1970) and Davies *et al.* (1972) did not employ computer fitting of functions to their data and determined the half times using plotting procedures. Thus, some error could be introduced in the analysis of gas exchange kinetics using these techniques. The difference could be species related as well.

The half times for HR and  $\text{VO}_2$  at the onset of exercise in the pony are appreciably faster than those reported for man (Diamond *et al.*, 1977; Powers *et al.*, 1985; Hughson, 1982). As mentioned previously, it seems likely that the half time of oxygen uptake in the pony during light exercise is influenced by the rapid "cardiodynamic" phase of gas exchange and therefore is not totally reflective of intramuscular events. Thus, in the transition from one work rate to another, no great change in the rate of  $\text{VO}_2$  kinetics would be expected. This appeared to be the case in the present experiments. Similar conclusions have been reached using human subjects (Diamond *et al.*, 1977). Finally, the findings that the half time of the  $\text{VO}_2$  response increases as the work rate increases is in agreement with work by Whipp and Wasserman (1972) and Hagberg *et al.* (1978). The relatively slower rate of  $\text{VO}_2$  adjustment seems reasonable in view of the fact that

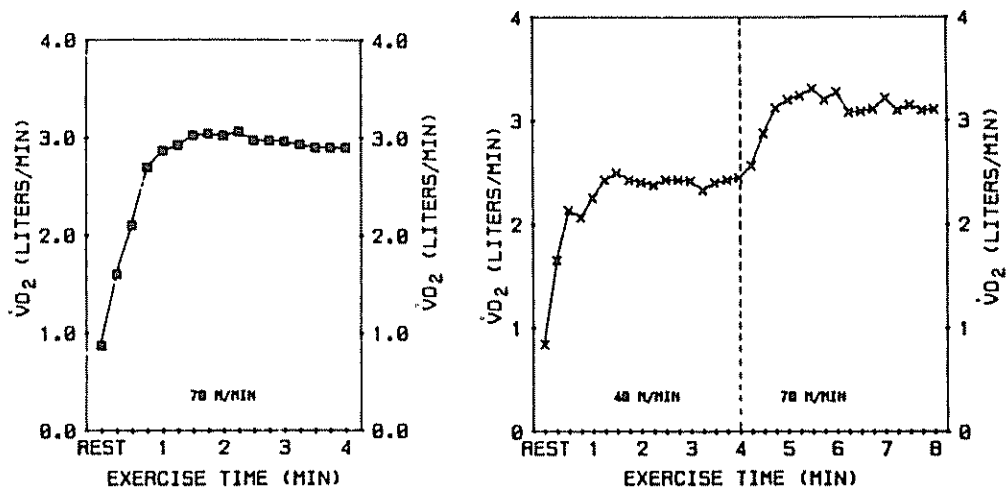


FIGURE 5. Temporal pattern of oxygen uptake ( $\dot{V}O_2$ ) during treadmill exercise in the two experimental protocols. The graph on the left represents  $\dot{V}O_2$  changes during the transition from rest to steady state exercise at 7% grade, 70 m/min. The graph on the right represents the change in  $\dot{V}O_2$  during the transition from rest to steady state exercise at 7% grade, 40 m/min and during the work-to-work transition (7% grade, 40 m/min to 7% grade, 70 m/min).

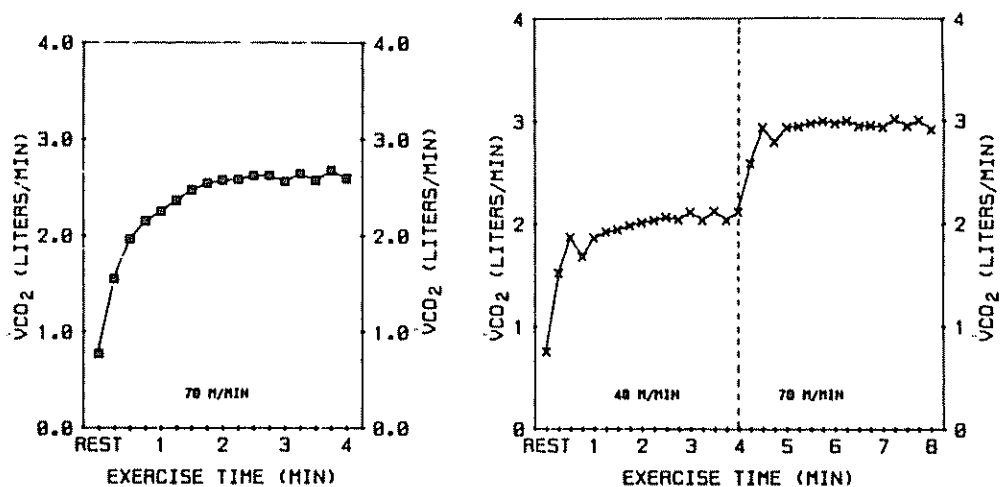


FIGURE 6. Changes in expired carbon dioxide ( $\dot{V}CO_2$ ) during treadmill exercise in the pony. The graph on the left represents  $\dot{V}CO_2$  changes in the transition from rest to steady state exercise at 7% grade, 70 m/min. The figure on the right represents the change in  $\dot{V}CO_2$  in the transition from rest to steady state exercise at 7% grade, 40 m/min and during the work-to-work transition, i.e. 7% grade, 40 m/min to 7% grade, 70 m/min.

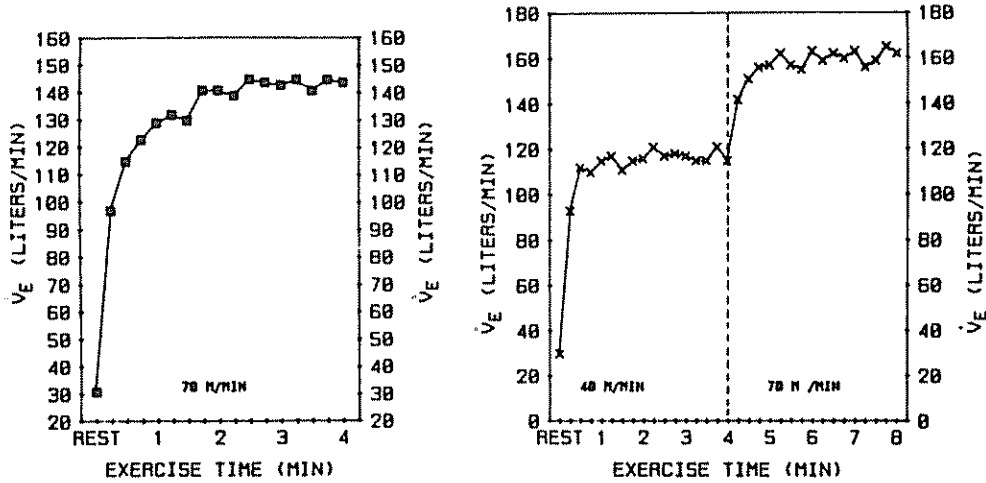


FIGURE 7. Temporal pattern of expired ventilation ( $V_E$ ) during treadmill exercise in ponies. The figure on the left represents the change in  $V_E$  during the transition from rest to steady state exercise at 7% grade, 70 m/min. The graph on the right represents the change in  $V_E$  during the transition from rest to steady-state exercise at 7% grade, 40 m/min and during the work-to-work transition (7% grade, 40 m/min to 7% grade, 70 m/min).

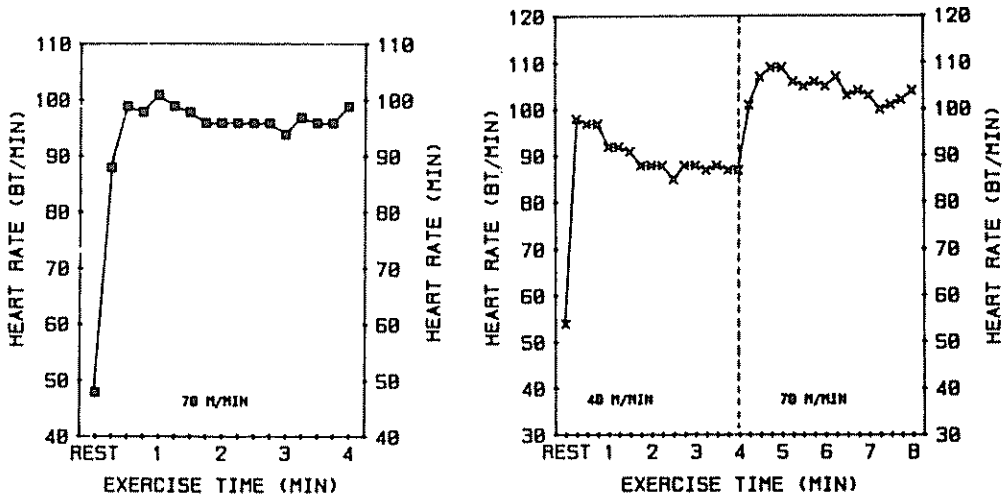


FIGURE 8. Heart rate (HR) kinetics during treadmill exercise in ponies. The figure on the left represents the change in HR during the transition from rest to steady state exercise at 7% grade, 70 m/min. The graph on the right represents the change in HR from rest to 7% grade, 40 m/min and during the work-to-work transition, i.e. 7% grade, 40 m/min to 7% grade, 70 m/min.

TABLE 2. Half times for oxygen uptake ( $\dot{V}O_2$ ), expired carbon dioxide ( $\dot{V}CO_2$ ), expired ventilation ( $\dot{V}_E$ ), and heart rate (HR) during the transition from rest to exercise and in the transition from one level of exercise to a higher level

Variable	Transition Period		
	rest-40 m/min <sup>1</sup>	40-70 m/min <sup>2</sup>	rest-70 m/min <sup>3</sup>
$\dot{V}O_2$	7.7 ± 1.6	6.4 ± 1.0 <sup>a</sup>	13.5 ± 1.8 <sup>b</sup>
$\dot{V}CO_2$	9.6 ± 2.3	7.4 ± 2.0	13.1 ± 1.6
$\dot{V}_E$	6.8 ± 0.9	12.8 ± 3.0	10.1 ± 1.7
HR	4.5 ± 1.3	5.3 ± 0.7	8.3 ± 1.4

Values are means ± SEM expressed in seconds

<sup>a</sup>statistically different ( $P < 0.05$ ) from rest, 70 m/min

<sup>b</sup>statistically different ( $P < 0.05$ ) from rest, 40 m/min and 40-70 m/min

<sup>1</sup>Transition period is from rest to steady state treadmill exercise at 7% grade, 40 meters/min

<sup>2</sup>Transition period is from steady state treadmill exercise at 7% grade, 40 meters/min to steady state exercise at 7% grade-70 meters/min

<sup>3</sup>Transition period is from rest to steady state treadmill exercise at 7% grade, 70 meters/min

the cardiodynamic phase of gas exchange would likely contribute a smaller portion of the total  $\dot{V}O_2$  half time during moderate exercise when compared to light work. In addition, Hagberg *et al.* (1978) have argued that higher work rates require greater changes in circulatory, respiratory, and metabolic adaptations and therefore are likely to produce longer  $\dot{V}O_2$  half times even when measured via respiratory gas exchange.

*$\dot{V}CO_2$  kinetics.* The half times for carbon dioxide kinetics reported in Table 2 for ponies are appreciably shorter than the average  $\dot{V}CO_2$  half time reported for humans i.e. human  $\dot{V}CO_2$  half time = 45 sec; Diamond *et al.*, 1977. This difference is likely due to a more rapid increase in cardiac output and ventilation at the onset of exercise in ponies when compared to humans (Pan *et al.*, 1983; Pan *et al.*, 1984; Forster *et al.*, 1984). In the present experiments, considerably more interindividual variability in  $\dot{V}CO_2$  kinetics existed than in  $\dot{V}O_2$  kinetics (Table 2). Similar findings have been reported in humans (Diamond *et al.*, 1977; Whipp *et al.*, 1982; Hughson and Morrissey, 1982). Although carbon dioxide kinetics were not significantly different ( $P > 0.05$ ) between treatments, the half times tended to be lower in the work-to-work transition when compared to both rest-to-work transitions. A possible explanation for this trend may be related not to an actual change in the kinetics of muscle carbon dioxide production, but to the reduced capacity of the body to store carbon dioxide at an elevated tissue carbon dioxide tension (Jones and Jurkowski, 1979). This would lead to a greater excretion of carbon dioxide for a constant increment of carbon dioxide production (Hughson and Morrissey, 1982).

### Conclusion

These data suggest that a monoexponential function is adequate to describe the rate of change of  $\dot{V}O_2$ ,  $\dot{V}CO_2$ ,  $\dot{V}_E$  and HR during the transition from rest to light exercise in the pony. The kinetic responses of  $\dot{V}CO_2$ ,  $\dot{V}_E$ , and HR were unaffected by exercise intensity or whether the transition was made from rest or from prior exercise. Further,

with similar metabolic increments, the rate of  $\dot{V}O_2$  adaptation from rest to exercise was not significantly different ( $P > 0.05$ ) from the  $\dot{V}O_2$  time course during the transition from one work rate to a higher work rate. In contrast, the  $\dot{V}O_2$  half times were significantly greater ( $P < 0.05$ ) in the transition from rest to 70 m/min when compared to a rest to 40 m/min transition. It is hypothesized that the half time of  $\dot{V}O_2$  in the pony during light exercise is principally influenced by the cardiodynamic phase of gas exchange and thus does not reflect oxygen uptake by the muscle. Therefore, the finding that  $\dot{V}O_2$  kinetics differs as a function of work rate should not be interpreted as a direct indication of differences in the rate of muscle metabolism.

## References

- Auchincloss, J., Gilbert, R. and Baule, G. (1966). Effect of ventilation on oxygen transfer during early exercise. *J. Appl. Physiol.* **21**, 810–818.
- Bisgard, G., Forster, H., Byrnes, B., Stanek, K., Klein, J., and Manohar, M. (1978). Cerebrospinal fluid acid base balance during muscular exercise. *J. Appl. Physiol.* **45**, 94–101.
- Daniel, C., and Wood, F. (1980). *Fitting Equations to Data*, Wiley, New York, pp. 1–95.
- Davies C., di Prampero, P. and Ceretelli, P. (1972). Kinetics of cardiac output and respiratory gas exchange during exercise and recovery. *J. Appl. Physiol.* **32**, 618–625.
- Diamond, L., Casaburi, R., Wasserman, K. and Whipp, B. (1977). Kinetics of gas exchange and ventilation in transitions from rest or prior exercise. *J. Appl. Physiol.* **43**, 704–708.
- di Prampero, P., Davies, C., Ceretelli, P. and Margaria, R. (1970). An analysis of  $O_2$  debt contracted in submaximal exercise. *J. Appl. Physiol.* **29**, 547–551.
- Forster, H., Pan, L., Bisgard, G., Dorsey, S. and Britton, M. (1984). Temporal pattern of pulmonary gas exchange during exercise in ponies. *J. Appl. Physiol.* **57**, 760–767.
- Hagberg, J., Nagle, F. and Carlson, J. (1978). Transient  $O_2$  uptake response at the onset of exercise. *J. Appl. Physiol.* **44**, 90–92.
- Hays, W. (1973). *Statistics for the Social Sciences*. Holt, Rinehardt, and Winston, New York, pp. 524–580.
- Henry, F. (1951). Aerobic oxygen consumption and alactic debt in muscular work. *J. Appl. Physiol.* **3**, 427–438.
- Hughson, R. and Morrissey, M. (1982). Delayed kinetics of respiratory gas exchange in the transition from prior exercise. *J. Appl. Physiol.* **52**, 921–929.
- Jones, N. and Jurkowski, J. (1979). Body carbon dioxide storage capacity in exercise. *J. Appl. Physiol.* **46**, 811–815.
- Linnarsson, D. (1974). Dynamics of pulmonary gas exchange and heart rate changes at start and end of exercise. *Acta Physiol. Scand. Suppl.* **455**, 1–68.
- Pan, L., Forster, H., Bisgard, G., Kaminski, R., Dorsey, S. and Busch, M. (1983). Hyperventilation in ponies at the onset of and during steady-state exercise. *J. Appl. Physiol.* **54**, 1394–1402.
- Pan, L., Forster, H., Bisgard, G., Dorsey, S. and Busch, M. (1984). Oxygen transport in ponies during treadmill exercise. *J. Appl. Physiol.* **57**, 744–751.

- Powers, S., Dodd, S. and Beadle, R. (1985). Oxygen uptake kinetics in trained athletes differing in  $\dot{V}O_2\text{max}$ . *Eur. J. Appl. Physiol.* **54**, 306–308.
- Powers, S., Lawler, J., Thompson, D. and Beadle, R. (1987). Measurement of oxygen uptake in the non-steady-state. *Aviat. Space Environ. Med.* In Press.
- Wasserman, K., Whipp, B. and Castagna, J. (1974). Cardiodynamic hyperpnea: hyperpnea secondary to cardiac output increase. *J. Appl. Physiol.* **36**, 457–464.
- Weissman, M., Jones, P., Oren, A., Lamarra, N., Whipp, B. and Wasserman, K. (1982). Cardiac output increase at the start of exercise. *J. Appl. Physiol.* **52**, 236–244.
- Whipp, B. (1971). Rate constant for the kinetics of oxygen uptake during light exercise. *J. Appl. Physiol.* **30**, 261–263.
- Whipp, B. and Wasserman, K. (1972). Oxygen uptake kinetics for various intensities of constant-load work. *J. Appl. Physiol.* **33**, 351–356.
- Whipp, B. and Mahler, M. (1980). Dynamics of pulmonary gas exchange during exercise. In: *Pulmonary Gas Exchange*, West, J. (ed.) Academic Press, New York, pp. 33–96.