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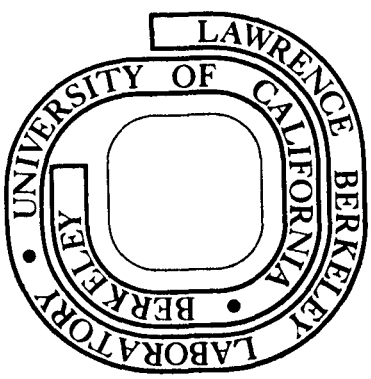

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Metabolic and Cardiac Frequency Responses of Laboratory Rats to Treadmill Exercise

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Running Head: Rat $\dot{V}O_2$, $\dot{V}CO_2$, and f_H in Exercise

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Abstract

A rapid flow, open circuit, indirect calorimeter was used to study metabolic rates and cardiac frequencies of rats at rest and in response to three running speeds (14.3, 28.7, and 43.1 m/min) and five slopes (1, 5, 10, 15 and 20%). Validity of the system was established by observing responses to the addition of mixed gases including $^{14}CO_2$, and by comparing oxygen consumptions determined when anesthetized rats were placed in the open or a closed circuit system. Half response time of the system was 27 sec. With one rat in each system, O_2 consumptions were 3.631 $\pm$ 0.206 and 3.677 $\pm$ 0.388 ml/min for the open and closed systems, respectively. With two rats, values were 8.275 $\pm$ 0.236 and 8.247 $\pm$ 0.454 ml/min for the open and closed systems. Highest values of $\dot{V}O_2$ observed were 17.95 $\pm$ 0.55 ml/min for 222 $\pm$ 7 g rats running at 43.1 m/min on a 20% slope. The corresponding f_H was 595$\pm$ 5 bpm. Correlations between $\dot{V}O_2$ and external work ranged from .88 on a 1% grade, to .93 on a 20% grade. Corresponding correlations between $\dot{V}O_2$ and f_H were .81 and .86, respectively. "Apparent" muscular efficiencies (calculated as the inverse of the slope of $\dot{V}O_2$ on work) were 20.5, 22.0, and 26.4 percent for animals running at 14.3, 28.7, and 43.1 m/min, respectively. "Gross" muscular efficiencies ranged from 1.29 to 4.47%. Results indicate that the metabolic response to increments in speed is much greater than to increments in grade.

Key words: Small animals, exertion, metabolism, energetics, efficiency, muscle, rodent.

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INTRODUCTION

Open circuit, indirect calorimetry has been used extensively to estimate metabolic rates of humans and large experimental animals. Systems for determination of oxygen consumption ($\dot{V}O_2$) in small animals have been suggested (10, 14, 18), but these systems have been limited in their ability to determine carbon dioxide production ($\dot{V}CO_2$) or applicability for use in conjunction with systems where external work rate could be quantified. In view of long recognized effects of training on the cardio-vascular system, and recent work which describes increases in skeletal muscle respiratory capacity (12) and muscle fiber adaptations in response to physical training (2, 21), it is important to describe heart rate (f_H), $\dot{V}O_2$, and $\dot{V}CO_2$ in the intact rat during controlled exercise. Further, in view of the power possessed by isotope tracer techniques for the study of metabolism, it is important to quantify the production of $^{14}CO_2$ following infusion of ^{14}C tracers. Here we describe a system for determination of oxygen consumption, carbon dioxide production, carbon dioxide specific activity, and heart rate in rats at rest or during treadmill running.

METHODS

Description of Apparatus. A bottomless plexiglass chamber (9.5 cm x 32.5 cm x 11.5 cm) (Figure 1; B) was designed to fit into one stall of a Quinton Rodent Treadmill (model 42-15). Electrified prods (Figure 1; B1) protrude 4.5 cm into the rear of the chamber, with variable voltage provided from the shocking powerstat of the treadmill. The chamber has a double ceiling, with a 9 mm space separating the two. The lower ceiling (Figure 1; B2) has 64 evenly spaced 3mm holes and acts as a manifold. Tygon tubing is attached to the air outlet (Figure 1; B3).

Fig. 1

Transverse support bars are placed across the top of the chamber, so that the chamber's weight is supported on adjacent treadmill stalls. Belt-chamber clearance approximates 2 mm at the front, and the bottom edges of the chamber are in contact with the belt along the sides and back. This allows for entrance of ambient air into the chamber and a unidirectional flow by the animal. The outlet tubing connects to a needle valve (Figure 1; C), flow meter (Figure 1; D) (Gilmont D-216), and then to the inlet side of a Universal Electric pump (Figure 1; E). Flow is regulated to 5000 ml/min STPD. Following the flow meter, a "T"-tube directs 4500 ml/min to a fume hood (Figure 1; O) as waste, while 500 ml/min are passed thru $CaSO_4$ (Figure 1; F) for dehydration preparatory to gas analysis. Beckman LB-2 CO_2 (Figure 1; G) and Applied Electrochemistry S-3A O_2 (Figure 1; H) sensors are connected in series with an applied electrochemistry R-1 flow control (Figure 1; K), which contains a flow meter, needle valve and pump (Figure 1; K1 and K2, respectively). The digital output of both analyzers is recorded on a Brush 440 recorder (Figure 1; J). The recorder is calibrated to give 0.5% full scale deflection for both O_2 and CO_2 (Figure 2). Following analysis, the 500 ml/min. flow is directed to a series of twelve CO_2 trapping columns with individual stopcocks (Figure 1; L, N). These columns can be filled with 50 ml of ethanolamine-methylcellusolve (1:2, v:v) (Figure 1; M) and permit the continual quantification of $^{14}CO_2$ evolution following infusion of ^{14}C tracers into experimental animals.

Fig. 2

Coiled ECG leads, made from cotton-covered manganim, are available inside the chamber for connection to subdermally implanted copper wire electrodes on the rat (transthoracic placement with ground above tail). ECG is recorded on a third channel of the Brush recorder following ampli-

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fication on a Brush Universal ECG (12-4218) amplifier (Figure 1; I, Figure 2).

Calculations. Oxygen consumption ($\dot{V}O_2$) and carbon dioxide production ($\dot{V}CO_2$) were calculated essentially as described by Consolazio (4) for humans using the premise of pulmonary N_2 equality in ventilation and the Haldane transformation.[1]

$$\dot{V}O_2 = \dot{V}_E \text{ STPD} \left[\frac{100 - \left(F_E CO_2 + F_E O_2\right)}{F_I N_2} \frac{F_I O_2}{100} - \frac{F_E O_2}{100} \right]$$

$$\dot{V}CO_2 = \dot{V}_E \text{ STPD} \left[\frac{F_E CO_2}{100} - \frac{100 - \left(F_E CO_2 + F_E O_2\right)}{F_I N_2} \frac{F_I CO_2}{100} \right]$$

Respiratory exchange ratio (R) was calculated as $\dot{V}CO_2/\dot{V}O_2$. Cardiac frequency f_H was obtained from the recorder tracing, knowing paper speed, QRS wave count for ten seconds, and extrapolating to a minute value. External work during treadmill running was expressed in kgm/min and defined as: (Speed (m/min)) $\left(\frac{\%\ \text{slope}}{100}\right)$ (Body wt (Kg)).

Muscular efficiency was calculated in two ways. "Apparent" efficiency was calculated as the inverse of the linear slope relating caloric equivalent of $\dot{V}O_2$ (5.047 cal/ml O_2) and caloric equivalent of external work performed (2.342 cal/kgm) (5). This definition of efficiency, as applied to rats during treadmill running, is similar to the "instantaneous", "work" and "delta" efficiencies employed in previous studies of humans (7, 9). "Gross" efficiency was calculated as the ratio of caloric equivalent of external work performed to caloric equivalent of oxygen consumption.

Calibration and Validation. The gas analyzers were calibrated before, during and after an experimental period using tank gases

previously established by the Scholander micro-technique. In this and other studies we have observed these analyzers to maintain calibration over four hours.

A variety of experiments were performed to determine if loss of expired gas at the bottom of the chamber could affect results. The metabolic chamber (chamber flow 5000 ml/min, analyzer flow 500 ml/min) was sealed at the bottom by placing it in 1.25 cm of water. A bypass "U-tube" was included to allow 5000 ml/min flow of ambient air into the chamber. Calibration gas of known composition was bled into the chamber through a small tube at a rate to produce a 0.5% increase in CO_2 and a similar decrease in O_2. The chamber was then removed from the water and placed on a motionless treadmill. The "U-tube" was removed but flow of calibration gas was maintained. The CO_2 and O_2 values observed with the chamber on the treadmill did not deviate from those observed over H_2O, thereby establishing that insignificant gas exchange occurs at the chamber bottom. To determine the effect of belt movement, the treadmill was turned on and gas values were observed over a ten minute period. This procedure was repeated with 2.8 m/min increments in speed over the range of speeds of the treadmill (0 to 58 mmin). Transient fluctuations were observed at the onset and offset of belt movement, but no systematic change in observed gas values occurred due to belt speed.

The half response time of the system for gas analysis was established by two methods. First, the response to the admission of known gases into the chamber was recorded. Second, the response time of the total system (including trapping columns) was assessed by bleeding a known amount of $^{14}CO_2$ into the metabolic chamber and quantifying the appearance of radioactivity in the traps. For this procedure $^{14}CO_2$ was generated

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by reacting $Ba^{14}CO_3$ with H_2SO_4 and trapping the $^{14}CO_2$ evolved in a 50 liter mylar bag which was then filled with a mixture of 0.5% CO_2 and 20.5% O_2. The $^{14}CO_2$ gas mix was bled into the metabolic chamber at a controlled rate. Gas was trapped sequentially in individual columns for one minute. This procedure was repeated five times.

A series of experiments was conducted using lightly anesthetized Wistar rats (sodium pentobarbital, 30 mg/kg) to compare $\dot{V}O_2$ values obtained with the open circuit system and a closed circuit system. A Collins 9 L respirometer was joined in a closed circuit with a glass bell jar (to house animals) and a pump to circulate gas through the system. Pairs of animals were anesthetized, with one animal placed in the closed system and the other in the open system. Forty minutes were allowed for equilibration of both systems, followed by a 40 minute assessment of $\dot{V}O_2$. At the end of the 80 minute procedure, the animals were exchanged between systems and the protocol was repeated. Ten repetitions were performed using different animals on different days. To achieve the effect of increasing the number of METS within the chambers, this protocol was repeated with two animals simultaneously in each system, the maximum number which could be accommodated.

Exercise protocol. Five female Wistar rats (Simonson Labs, Gilroy, California), two months old, were used in a series of experiments to assess the affect of running speed and slope on $\dot{V}O_2$, $\dot{V}CO_2$, and f_H. These rats were fed ad libitum on laboratory rat chow (Feedstuffs Processing, San Francisco) and were housed in separated cages maintained on a 12h/12h, 6:00 AM/6:00 PM), light/dark cycle. These rats were participating in a conditioning regime in accordance with the protocol of Holloszy (12), and were currently training at 8° slope, 1.1 mph for 60 to 75 min/day, 5 days/week. In addition, rats were familiar with running

inside the metabolic chamber. On five separate occasions, at least one day apart, rats ran continuously at three incremental speeds (14.3, 28.7 and 43.1 m/min), with the slope held constant at either 1,5,10,15 or 20%. The order of slopes was systematically adjusted among rats to minimize training effects. During any given experiment an animal was given a three minute rehabituation run inside the chamber at 14.3 m/min, 1% slope. The exercise was momentarily stopped while the ECG leads were attached to recording clips. Exercise then continued for seven additional minutes at 14.3 m/min, five minutes at 28.7 m/min, and five minutes at 43.1 m/min. The Brush recorder speed was adjusted to 5 mm/min during the majority of exercise. Respiratory parameters were calculated from values recorded during the last minute of each work intensity. At the end of each work increment, while the rat continued running, the recorder chart speed was increased to 5 mm/sec to record separate QRS waves (Figure 2).

RESULTS

Results of the experiments to recover $^{14}CO_2$ added to the metabolic chamber (Figure 3) indicate rapid equilibration within the system. The half response time was 27 sec. Similar kinetics were observed in deflections of O_2 and CO_2-content tracings when rats were inserted into, or removed from the chamber.

Fig. 3

Experiments to validate $\dot{V}O_2$ determinations in the open system with the closed system indicate a close correspondence of results (Table 1). A difference in mean O_2 consumption values of 1.27% was observed between the open and closed systems with one rat in each. When this protocol was repeated with two rats simultaneously in each system, the mean O_2 consumptions differed by only 0.34%. Neither of the differences reached statistical significance ($p < .05$). The data are consistent

Table 1

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with those obtained previously by Denckla (6) on resting female rats.

Summarized data of $\dot{V}O_2$, R, f_H, body weight, and external work performed by the exercising rats are given in Table 2. The relationship between caloric equivalent of O_2 consumed and caloric equivalent speed of running on a constant grade in exercising rats (Figure 4) appears increasingly non-linear as the inclination of running is increased. A similar trend is apparent in the relationship between heart rate and speed on constant grade (Figure 5).

Table 2

Fig. 4

Fig. 5

Correlation coefficients between $\dot{V}O_2$ and external work, between $\dot{V}O_2$ and f_H, and between f_H and external work, are expressed both as a function of speed at any given slope, and as a function of slope at any given speed (Table 3). The correlations with speed at any given slope are higher (range .69 to .93) than the correlations across slope at each speed (range .21 to .68).

Table 3

Calculated "apparent" muscular efficiency (Table 4A) increases as a function of running speed, but for a given external work output (eg., 1 cal.), the metabolic rate at higher running speeds is greater than at slower running speeds (Figure 4). The calculated "gross" muscular efficiencies, therefore, decrease as speed increases (Table 4B).

Table 4

DISCUSSION

We have described a versatile rapid response system enabling quantification of metabolic rate of laboratory rats during treadmill exercise. In addition to allowing the assessment of metabolic and cardiac frequency responses under a wide range of exercises, the system lends itself to quantification of $^{14}CO_2$ evolution following ^{14}C tracer infusion. The strong regression between $\dot{V}O_2$ and f_H observed in this study should allow estimation of metabolic responses in rats without use of sensitive gas

analysis equipment (Table 3C).

Determinations of $\dot{V}CO_2$ and $\dot{V}O_2$ on rats during exercise in this study result in values of respiratory exchange which increase in response to external work load (Table 2). However, even at low workloads, R was seen to exceed unity. We attribute this result at low workloads to the excitement of animals during exercise. When placed on the treadmill to exercise, rats squealed and responded to easy exercise with uneven pacing. Evidence that the elevated values of R observed in this study were transitory and due to excitement is found in other data we have obtained on similar animals. Over two hours of observation values of R obtained at rest in these experiments declined from 0.93 to 0.81, at 14.3 m/min on a 1% slope, R declined from 1.00 to 0.88, and at 28.7 m/min on a 15% slope, R declined from 1.04 to 0.94. The low correlations between f_H and external work at lower work rates (Table 3) also support the conclusion of an effect of animal excitement.

Previous reports of the O_2 consumption response of small animals to variations in running speed are quite variable, and range from values 36% greater than those observed in the present study, to values 24% lower than those we observed (Figure 6). Direct comparisons among the various studies are difficult to make as variations in experimental treatment such as inclination of running, degree of conditioning, accuracy and stability of equipment, animal species, sex, size and strain, ambient temperature, and other factors may effect the results. In the present study, the O_2 consumptions at 1% inclination were 4.87, 6.05 and 6.67 ml $O_2 . 100g^{-1} . min^{-1}$ at speeds of 14.3, 28.7, and 43.1 m/min, respectively. These speeds and grades corresponded to external work rates of 3.18, 6.37 and 9.56 x 10^{-2} kgm/min. Shepherd and Gollnick (18) observed the

Fig. 6

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metabolic responses of rats in a running wheel. They noted a linear response between $\dot{V}O_2$ and wheel circumference speed up to 49.5 m/min, at which point the relationship plateaued. We calculated a linear regression from the portion of their mean data which appears linear, and found it to predict VO_2 values which averaged 31.9% greater than what we observed (Figure 6). One must be cautious in interpreting this variance, since speed of running and degree of inclination for a rat in a wheel are not known or held constant. Taylor, et al. (19) ran white rats at speeds of 6 to 23 m/min, with no mention of inclination or degree of training of the rats. Using his least squares linear regression, VO_2 values 17% lower than what we observed for rats running at 14.3 m/min are predicted. The slope of the curve relating VO_2 and running speed reported by Taylor, et al. is markedly steeper than that of our data or any other reported (Figure 6). If one extrapolates the data of Taylor, et al. to running speeds of 28.7 and 43.1 m/min, the predicted values vary -7.4% and +7.4% in comparison to our results at these speeds. In an elaborate investigation, Popovic, et al. (17) used rats which were preselected for running, but untrained. A linear regression calculated from their mean $\dot{V}O_2$ values observed at 10 and 20 m/min running speed predicts a value at 14.3 m/min which is 23.0% lower than what we observed. If we extrapolate their data to running speeds of 28.7 and 43.1 m/min, the slope of their relationship tends to parallel our data, but predicts values which are 25.6% and 21.0% lower than our observed values at these speeds.

The increasingly non-linear responses of $\dot{V}O_2$ (and $\dot{V}CO_2$) to speed of running at increasing inclinations is a curious observation (Table 2, Figure 4). It is likely that the plateau in $\dot{V}O_2$ (or at least the beginning of a plateau) at 43.1 m/min is a true break in linearity.

At any given slope, the animal may be approaching a $\dot{V}O_2$ max for that particular inclination. In humans $\dot{V}O_2$ max appears to depend on the amount of muscle mass involved in the exercise, up to some critical mass (1). It is possible that we observed higher values of $\dot{V}O_2$ at greater inclinations of running in rats due to an increased involvement of metabolically active tissue. This conclusion is consistent with related findings by others. One adaptation of skelatal muscle fibers to prolonged physical training is an increase in their oxidative capacity (2, 12). This adaptation seems to be dependent in part on the level of training (8). Terjung (21) has recently demonstrated an increased involvement of selected skeletal muscles as evidenced by an increase in citrate synthase in the rat hindlimb when rats were trained to run on a 30% slope versus a 10% slope.

Investigations of fiber recruitment have demonstrated in laboratory animals and in humans that there exist thresholds of exercise intensity that elicit orderly increments in muscle fiber recruitment. According to this size principle (11), increased work intensity would result in increased utilization of glycogenolytic, glycolytic muscle fibers for energy transduction. Recruitment of these glycogenolytic, glycolytic, non-oxidative, fibers could explain a non-linear response of $\dot{V}O_2$ to increments in work.

Popovic, et al. (17) have shown stroke volume in rats to be essentially constant during exercise which elicits a wide range of submaximal cardiac frequencies (365-523 bpm). At maximum cardiac output, assuming a-$\dot{v}O_2$ is maximum and constant, a decrease in cardiac frequency would be indicative of a decrease in oxygen consumption. The cardiac frequencies in response to external work observed in the present investigation (Figure

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5) demonstrate a small break in linearity at 5% slope, and further deviations from linearity as the inclination of running is increased to 20%. This effect of slope on f_H parallels that on $\dot{V}O_2$. Wranne and Woodson (23) reported a linear relationship between heart rate and speed during an incremental treadmill running regime administered to rats. Careful inspection of their data, however, demonstrates a break in linearity occuring at 15 min of exercise, which coincides with treadmill exercise at 26.8 m/min and 25° inclination. Barnard, et al. (3) have demonstrated a linear relationship between cardiac frequency and speed of level running. Our values determined at 1% inclination are consistent with that observation. However, their values are approximately 6.0% greater at the three running speeds the two studies share in common. This is not surprising since Barnard, et al. used untrained rats. Training-induced bradycardia is well documented for resting heart rates in rats (13, 22).

Another factor which may have produced non-linear relationships between $\dot{V}O_2$ and speed on constant slope, was the erratic pacing of rats at lower workloads. At lower speeds and slopes rats tend to utilize their power inefficiently and their running is accompanied by extraneous activity. As the work intensity increases, however, rats are forced to devote their energies to the external workload. Hence, the constancy of pacing and economy of motion at higher grades may give rise to the results of a non-linear relationship between $\dot{V}O_2$ and work, and a greater calculated "apparent" efficiency with increasing speed.

When considering effects of speed and inclination of running on muscular efficiency, one must be careful that the definition of efficiency utilized does not produce results that are at odds with the experimental data. As has been discussed previously (7, 9), use of the "apparent",

"delta", or similar definitions of efficiency minimize artifacts associated with baseline selection. However, in using a definition of efficiency based upon the regression of slope of $\dot{V}O_2$ on external work, one must be careful that a greater efficiency, calculated on the basis of a lesser slope, is not contradicted by a greater caloric cost, or lesser "gross" efficiency. We, therefore, have estimated efficiency by both "apparent" and "gross" definitions. We have observed a positive relationship between increasing "apparent" efficiency and speed (Table 4A, Figure 4). This observation is similar to that reported previously by Wunder (24) on red squirrels. His protocol included running at 15, 25 and 35 m/min on slopes of 6, 18, 30, and 37°. Applying the definition of "apparent" muscular efficiency to Wunder's data, we calculate efficiencies of 24.4, 28.0, and 31.2 percent at running speeds of 15, 25, and 35 m/min, respectively. This result is not consistent with results of gross efficiency calculations (Table 4B) or data obtained on humans during walking or cycling from which various investigators have concluded that speed decreases efficiency. Moreover, the energy cost response of running rats to increments in speed is much greater than to increments in grade (Table 4, Figure 4). For instance, compared to exercise at 14.3 m/min (15% grade), the performance of the equivalent of 1 calorie of external work at a speed of 43.1 m/min (5% grade) requires a 27.5% greater $\dot{V}O_2$. This economy by small animals in climbing inclines has been previously noted by Taylor, et al. (20).

Inspection of the data (Table 2, Figure 4) reveals two qualitative differences in metabolic responses of rats to changes in running speed and external work rate in comparison to data obtained on humans during walking (7). First, for humans the curves of caloric cost on work rate are exponentials in which increments in work require disproportionately

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greater VO_2 responses. With rats, however, there is no indication that the curves are increasing exponentially, but rather the curves tend to reach an asymptote parallel with the abscissa as work rate increases. Secondly, with humans, increments in speed have the effect of increasing VO_2 exponentially (e.g., in a plot of VO_2 against work rate at different speeds for humans during walking the y intercepts would be exponentially ordered with linear increments in speed), while with rats was observed that the increment in VO_2 for increasing speed to 43.1 m/min from 28.7 m/min was less than that for increasing speed to 28.7 from 14.3 m/min. These differences are probably in part related to differences in bipedal and quadrapedal forms of locomotion, and the transitions between walking to running and trotting to galloping. These differences may also be due to the relatively high resting metabolic rate in rats, the limited capacity of rats to expand $\dot{V}O_2$, and to the recruitment of glycogenolytic, glycolytic muscle fibers in hard exercise. If in the rat running at high speed the totality of ATP required for work is not derived from respiration, then the observations of an increased apparent muscular efficiency at high speeds, and the $\dot{V}O_2$ curves approaching asymptotes parallel with work rate as work rate increases may be explained.

Text Footnotes

1. Abbreviations used:

STPD - standard temperature and pressure, dry.

$\dot{V}O_2$ - volume of oxygen consumed per minute.

$\dot{V}CO_2$ - volume of carbon dioxide produced per minute.

$\dot{V}_E$ - volume of gas flowing from metabolism chamber per minute (includes animal's expired gas).

F_IO_2, F_ICO_2, F_IN_2 - Fractions of dry gas drawn into the metabolic chamber which are oxygen, carbon dioxide and nitrogen, respectively.

F_EO_2, F_ECO_2 - Fractions of dry gas drawn from metabolic chamber which are oxygen and carbon dioxide, respectively.

METS - Multiples of the resting metabolic rate.

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0 0 0 0 4 7 1 0 0 7 1

TABLE 1. Oxygen consumption of rats (ml/min) obtained in open- and closed-circuit indirect calorimeters. Values are averages recorded over forty minute observations.

A. One Rat

Rat	Circuit Open	Circuit Closed	BW (kg)
1	4.07	3.81	.199
2	3.43	2.75	.192
3	3.37	2.96	.200
4	2.86	2.64	.229
5	4.00	4.62	.220
6	3.00	3.16	.205
7	5.00	6.11	.365
8	3.50	3.82	.308
9	4.03	3.47	.222
10	3.05	3.43	.205
	$\bar{x}$=3.631	3.677	.235
	$S\bar{x}$ = .206	.328	.018
	t ratio = .255[+]		

B. Two Rats

Rat Pair	Circuit Open	Circuit Closed	Total BW (kg)
1	8.60	8.63	.470
2	7.57	7.96	.434
3	8.63	7.98	.454
4	8.77	8.20	.461
5	8.58	8.69	.426
6	7.50	8.02	.481
	$\bar{x}$=8.275	8.247	.454
	$S\bar{x}$=.236	.135	.009
	t ratio =	.143[++]	

[+] t = 2.262 required for significance at .05 confidence level.

[++] t = 2.571 required for significance at .05 confidence level.

TABLE 2. $\dot{V}O_2$, $\dot{V}CO_2$, f_H, R, body weights, and external work rates performed by exercising rats at specific speeds and slopes on a treadmill. n = 5 unless otherwise indicated. Values $\bar{x} \pm S\bar{x}$

Slope %	Speed ml/min	Body Weight kg	$\dot{V}O_2$ ml/min	$\dot{V}CO_2$ ml/min	R	f_H bpm	External Work Kgm/minx10^{-2}
1	14.3	.222±.009	10.82±.39	12.15±.54	1.12±.03	500.2±16.7	3.18±.12
	28.7	.222±.009	13.44±.51	15.40±.73	1.14±.03	531.2±16.9	6.37±.25
	43.1	.222±.009	14.79±.44	18.39±.67	1.24±.01	569.8±7.9	9.56±.37
5	14.3	.215±.008	11.30±.85	12.50±.60	1.12±.07	474.0±20.9	15.99±.62
	28.7	.215±.008	13.43±.61	15.39±.57	1.15±.06	519.8±14.6	30.87±1.10
	43.1	.215±.008	15.24±.74	18.91±.45	1.25±.05	564.4± 3.7	46.33±1.65
10	14.3	.218±.008	11.60±.53	12.80±.73	1.10±.03	483.4±13.5	31.20±1.13
	28.7	.218±.008	14.94±.64	17.35±.87	1.17±.02	532.8±14.5	62.54±2.26
	43.1	.218±.008	16.31±.90	19.27±.91	1.18±.02	574.8±15.7	93.87±3.40
15	14.3	.220±.008	11.99±.53	13.70±.80	1.14±.04	512.8±14.8	47.31±1.69
	28.7	.220±.008	15.24±.24	18.58±1.20	1.22±.07	563.0±13.2	94.85±3.39
	43.1	.220±.008	16.65±.37	20.70±.87	1.24±.04	591.5±10.6	143.00±5.58
20+	14.3	.222±.007	12.00±.42	14.06±.12	1.16±.02	508.5±22.8	63.54±2.06
+	28.7	.222±.007	15.66±.51	18.19±.53	1.16±.04	557.0±14.53	127.38±4.12
+	43.1	.222±.007	17.95±.55	22.38±.66	1.25±.04	595.0±5.00	191.17±6.18

+n = 4

0 0 0 0 4 7 1 0 0 7 2

TABLE 3. Correlation coefficients between $\dot{V}O_2$, external work, and f_H at specified speeds and slopes of running. Regression equations predicting $\dot{V}O_2$ from f_H are also presented.

A. Correlations as a function of speed at each slope:

Slope (%)	Pairs of Data	f_H and work	$\dot{V}O_2$ and work	$\dot{V}O_2$ and f_H
1	15	.72*	.88*	.81*
5	15	.78*	.82*	.69*
10	15	.82*	.87*	.83*
15	15	.78*	.92*	.81*
20	12	.74*	.93*	.86*

B. Correlations as a function of slope at each speed:

Speed (m/min)	Pairs of Data	f_H and work	$\dot{V}O_2$ and work	$\dot{V}O_2$ and f_H
14.3	24	.21	.42*	.43*
28.7	24	.41*	.65*	.67*
43.1	24	.50*	.68*	.55*

C. Regression equations for prediction of $\dot{V}O_2$ (y, in ml/min) from f_H(x, in bpm)

(1) Equations determined as a function of running speeds at each slope:

1%: $y = -7.025 + 0.038x$

5%: $y = -3.088 + 0.032x$

10%: $y = -8.372 + 0.043x$

15%: $y = -8.638 + 0.042x$

20%: $y = -11.673 + 0.049x$

(2) Equations determined as a function of slope at each running speed:

14.3 m/min: $y = 4.698 + 0.014x$

28.7 m/min. $y = -0.279 + 0.027x$

43.1 m/min: $y = -8.237 + 0.042x$

Correlation coefficients of .50, .45, and .35 are required for statistical significance ($p < .05$) with 10, 13, and 22 degrees of freedom, respectively.

TABLE 4. Efficiencies of running rats as calculated by "Apparent" and "Gross" definitions, expressed as a percent.

Definition of Efficiency	External Work Rate (cal/min)	Speed 14.3 m/min	28.7 m/min	43.1 m/min
A. Apparent[+]	-	20.46	21.98	26.42
B. Gross[++]	1.0	1.68	1.39	1.29
	2.0	-	2.64	2.45
	3.0	-	3.77	3.51
	4.0	-	-	4.47

[+]Apparent efficiency = 1/slope of regression of caloric equivalent of $\dot{V}O_2$ on caloric equivalent of external work performed.

[++]Gross efficiency = caloric equivalent of external work performed / caloric equivalent of $\dot{V}O_2$.

0 0 0 0 4 7 1 0 0 7 3

Figure Legends

Figure 1. Schematic diagram of metabolic chamber and ancillary equipment: A - rodent treadmill, B - metabolic chamber, B1 - electrified motivational prods, B2 - manifold, B3 - gas outlet, C - needle valve, D - flow meter, E - pump, F - $CaSO_4$, G - CO_2 sensor, H - O_2 sensor, I - preamplifiers, J - recorder, K - flow meter, K1 - needle valve, K2 - pump, L and N - CO_2 trapping columns, M - ethanolamine-methyl cellusolve, O - fume hood.

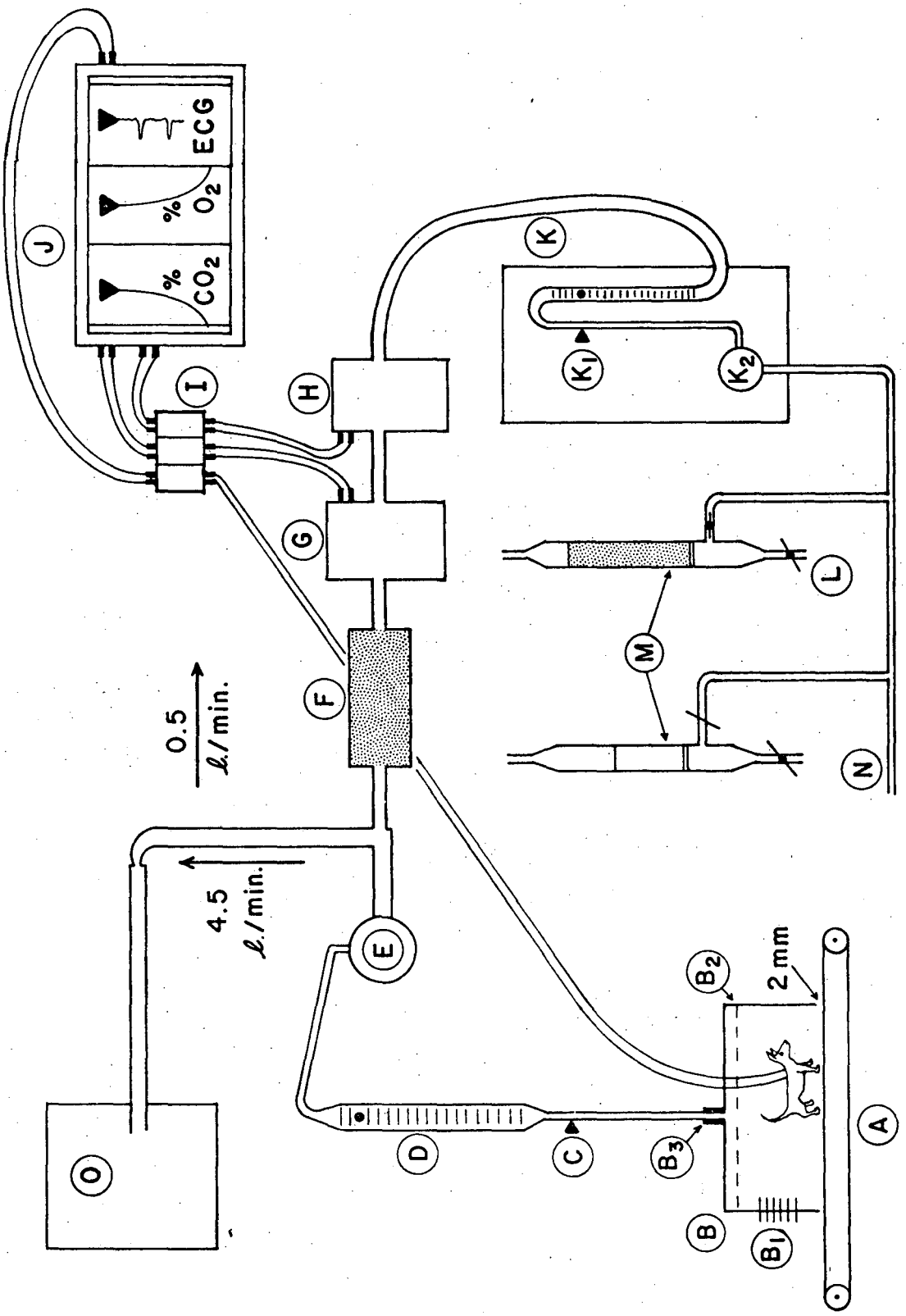
Figure 2. Sample of recorded values of F_EO_2, F_ECO_2, and f_H.

Figure 3. Equilibration of $^{14}CO_2$ added to the metabolism chamber, mean $\pm$ $S\bar{x}$ of five trials.

Figure 4. Caloric equivalent of $\dot{V}O_2$ plotted against the caloric equivalent of external work performed by exercising rats.

Figure 5. Cardiac frequency expressed as a function of external work performed by exercising rats.

Figure 6. Data from the present study regarding the effect of running speed on metabolic rate are plotted along with similar data obtained by other investigators including: Shepherd and Gollnick (18), Wunder (25), Taylor, et al. (19), and Popovic, et al. (17). Solid lines indicate reported data. Dashed line indicate linear extrapolations.



XBL 769-9552

Fig. 1

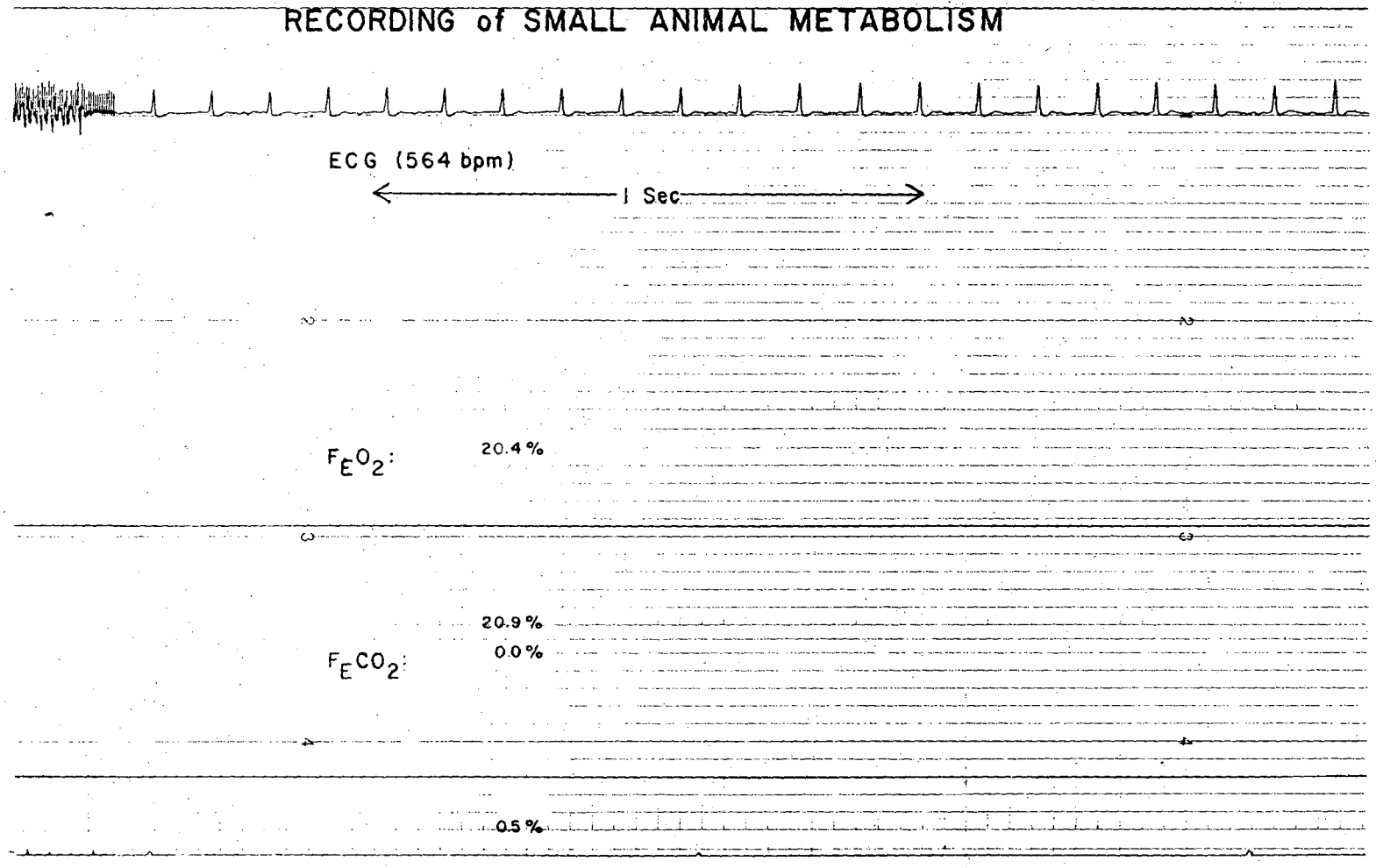
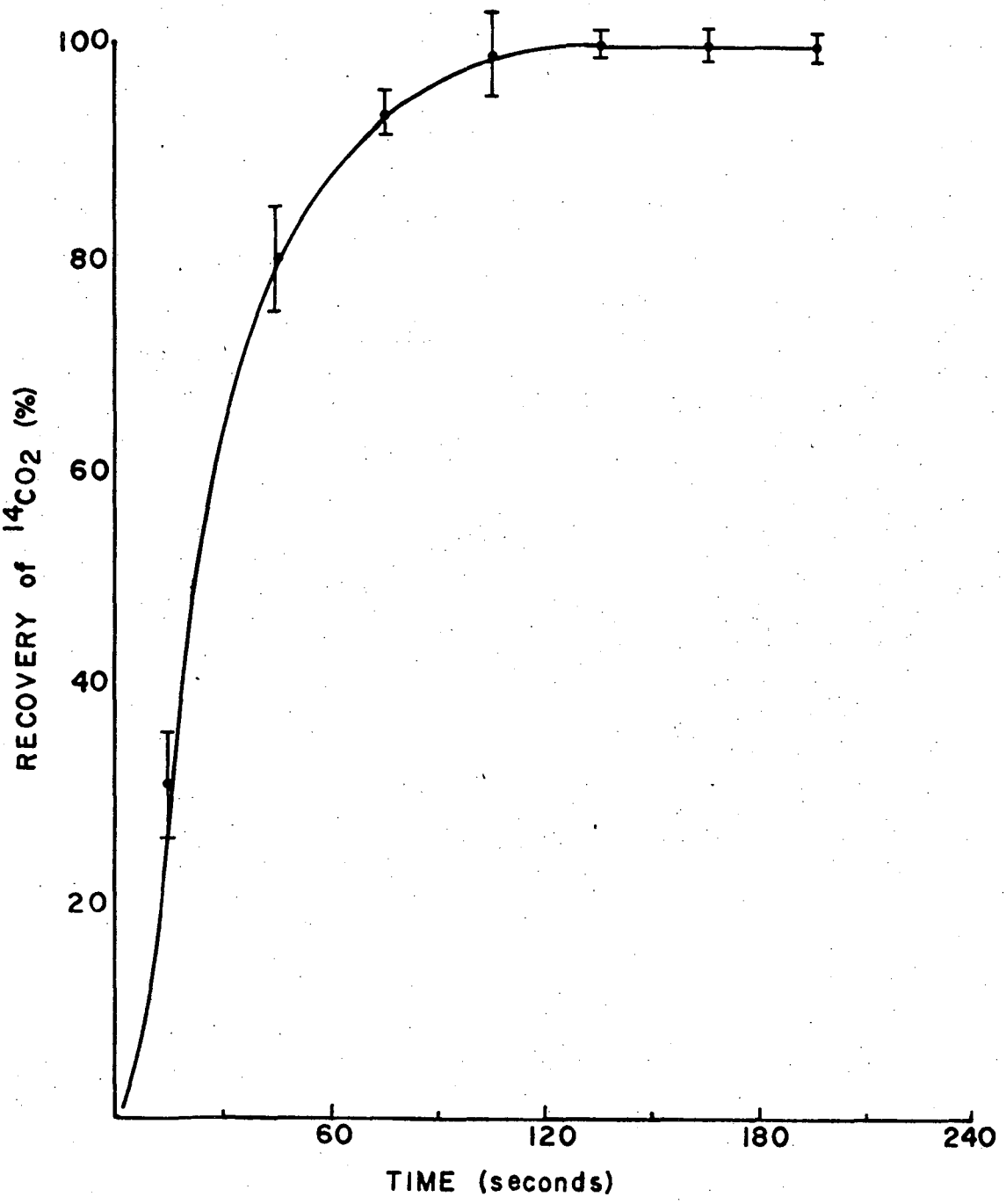


Fig. 2

0 0 0 0 7 4 1 0 0 7



XBL 773 - 4259

Fig. 3

0 0 0 0 4 7 1 0 0 7 5

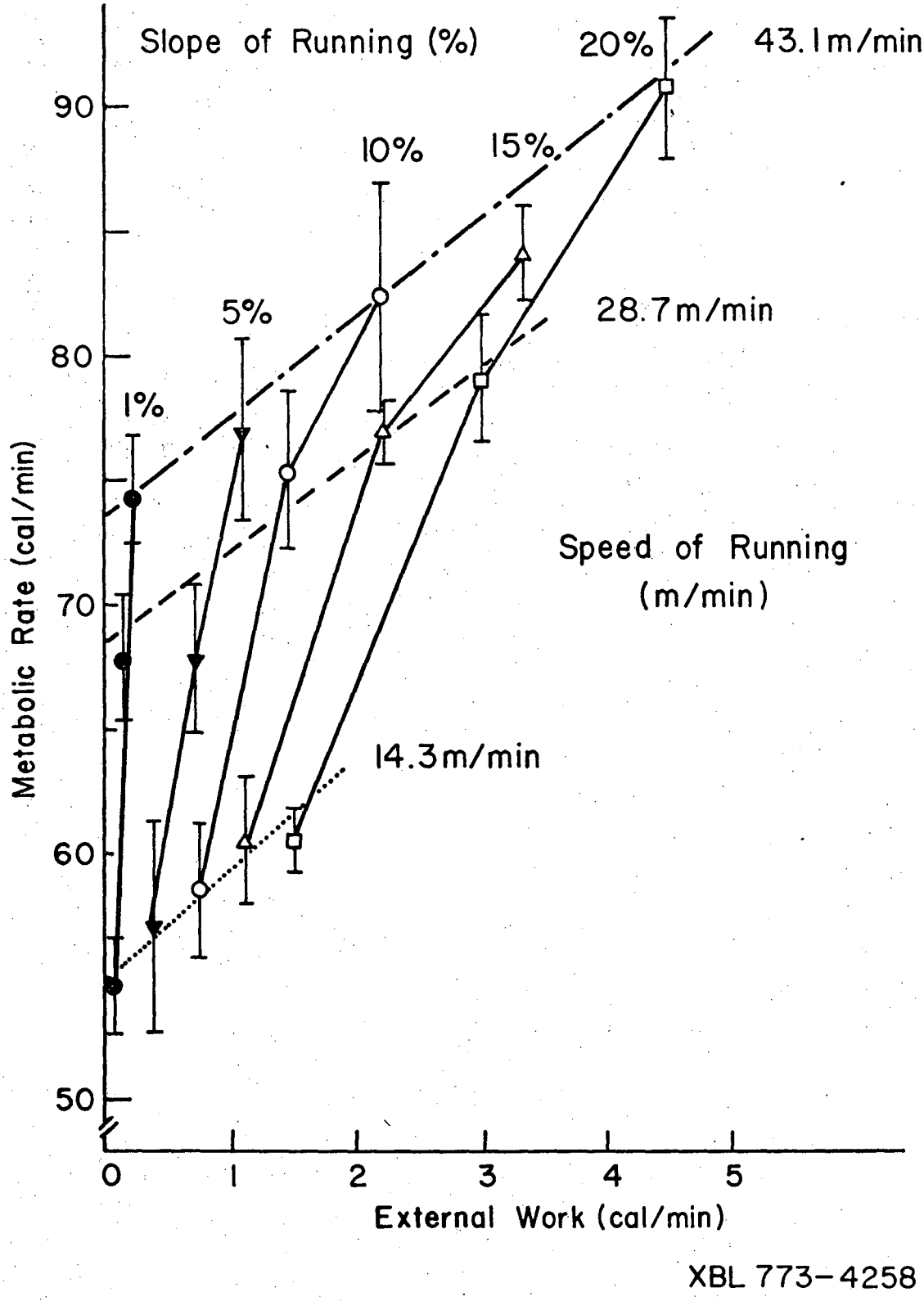


Fig. 4

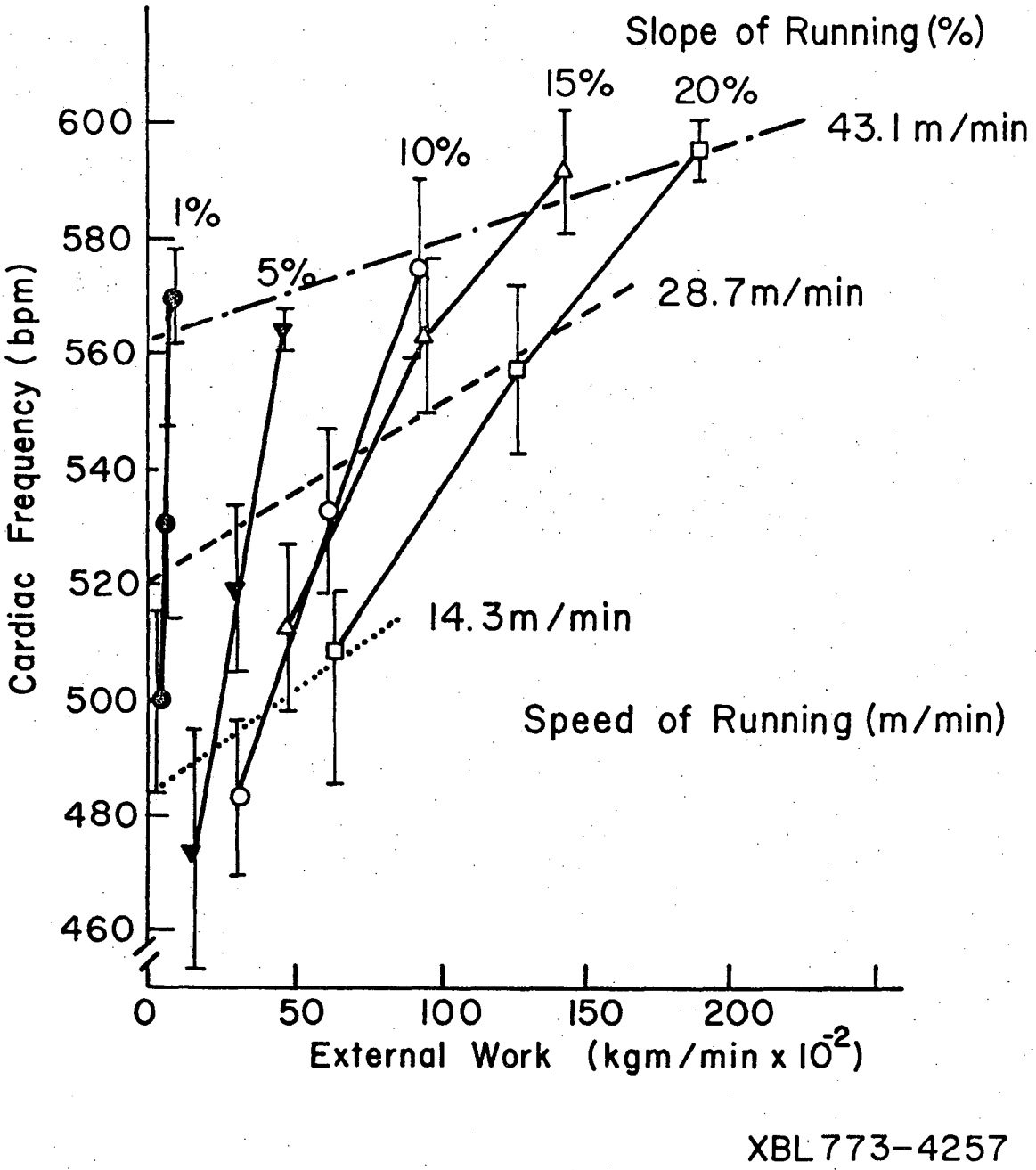

Slope of Running (%)
1%
5%
10%
15%
20%
43.1 m/min
28.7m/min
14.3m/min
Speed of Running (m/min)
Cardiac Frequency (bpm)
600
580
560
540
520
500
480
460
0
50
100
150
200
External Work (kgm/min x 10^-2)
XBL 773-4257

Fig. 5

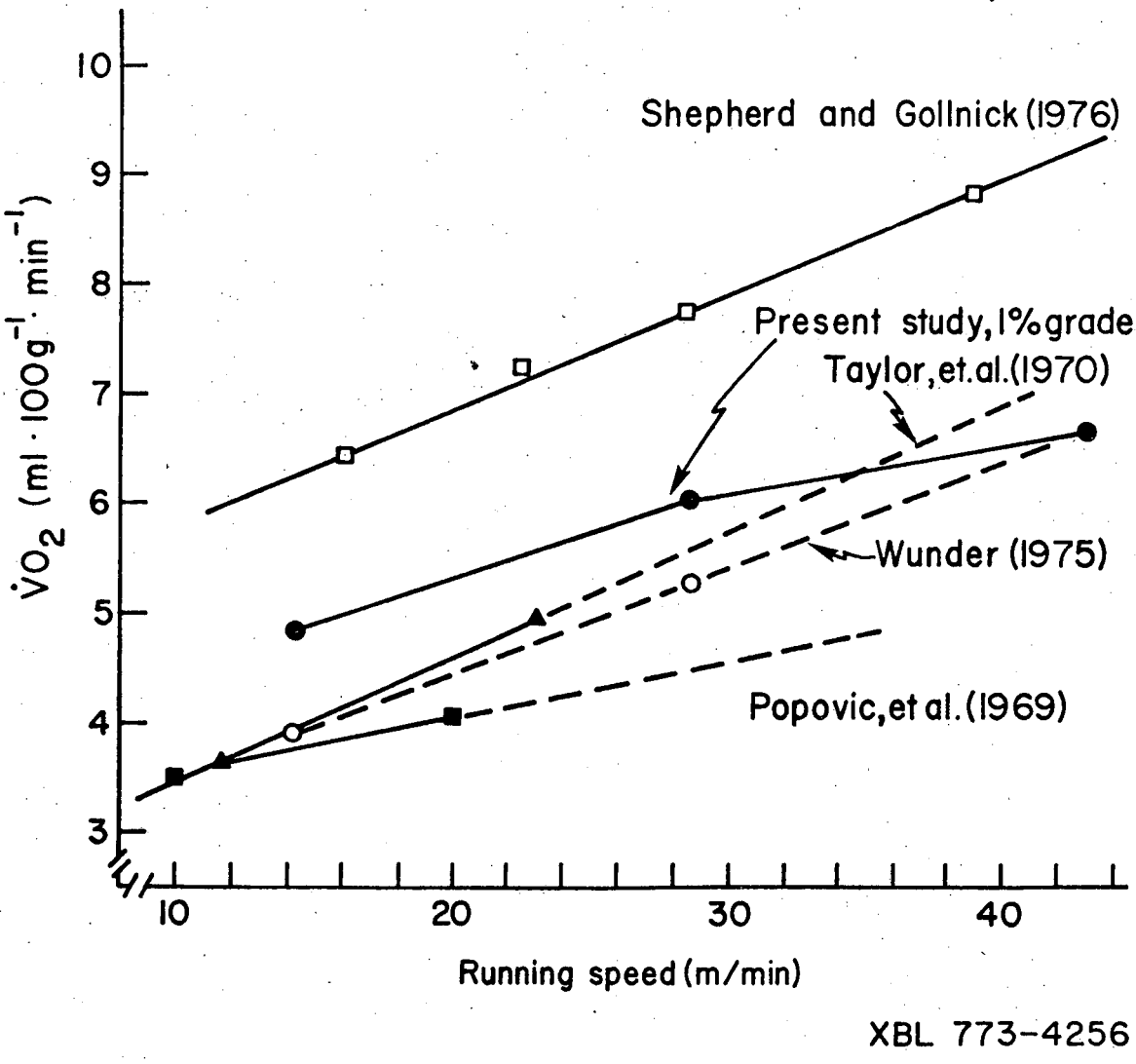

Shepherd and Gollnick (1976)
Present study, 1% grade
Taylor, et.al. (1970)
Wunder (1975)
Popovic, et al. (1969)
$\dot{V}O_2$ (ml · 100g^{-1} · min^{-1})
Running speed (m/min)
10
9
8
7
6
5
4
3
10
20
30
40
XBL 773-4256

Fig. 6

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