Reprinted from JOURNAL OF APPLIED PHYSIOLOGY
Vol. 14, No. 6, November, 1959
Printed in U.S.A.

Effect of time after feeding and carbohydrate or water supplement on work in dogs[1]

D. R. YOUNG, A. IACOVINO, P. ERVE, R. MOSHER AND H. SPECTOR
Quartermaster Food and Container Institute for the Armed Forces, U.S. Army, Chicago, Illinois

YOUNG, D. R., A. IACOVINO, P. ERVE, R. MOSHER AND H. SPECTOR. *Effect of time after feeding and carbohydrate or water supplement on work in dogs.* J. Appl. Physiol. 14(6): 1013–1017. 1959.—Effects of proximity of the last meal and post-absorptive supplementation with water or carbohydrate were examined in reference to aerobic work performance in the dog. In the first series, performance was measured utilizing a standard 40-minute period of treadmill running adjusted to a work load of 202.9 kg-m/min. administered 1½, 4, 6 and 24 hours following the intake of a normal meal. On the average, minute pulse rate was significantly nine beats higher and body temperature 0.75°F higher at 4 and 6 hours following the meal. There was no significant effect on energy expenditure due to specific dynamic action of the food. Maximum aerobic work capacity was studied. Provision of 1.5 liters of water during work markedly improved (+80%) performance, whereas provision of carbohydrate just prior to work was without immediate benefit. Increased work capacity due to water supplementation is mediated by the maintenance of a relatively normal state of hydration, improvements in temperature regulation and a beneficial effect on carbohydrate metabolism.

FREQUENCY OF MEALS and carbohydrate supplementation have been periodically examined for their influence on work performance. While the earlier data indicate that prior intake of food or supplementation with simple sugars is without benefit on subsequent work efficiency (1–7), more recent reports (8, 9) suggest a beneficial effect of certain meal components on subsequent capacity for work.

Theoretical arguments in support of the latter thesis advance the theory that work output is correlated with a rise in both blood sugar and respiratory quotient following a meal containing carbohydrate. Haggard and Greenberg (10, 11) have pursued this argument to the practical conclusion of recommending frequent feeding for maximum work efficiency.

At the other extreme, impairment of physical efficiency or loss in economy of work due to recent intake of food is suggested by the excess heat production resulting from the specific dynamic action of foods, particularly protein; diversion of blood flow from active muscles to the viscera, and the incidence of gastric distress during work following a meal.

The present experiments with dogs were designed to more fully evaluate the effect of proximity of the meal time on economy of work and to ascertain possible benefits to work performance in the post-absorptive state of water or carbohydrate supplements.

METHODS

The data presented here have been drawn from two series of experiments conducted with six male, purebred, beagle dogs 17 months of age (8.4–12.1 kg). These dogs had been maintained in a high state of physical conditioning for 7 months prior to testing and were well adjusted to the laboratory personnel and procedures. The animals were housed at all times in environmentally controlled animal rooms. Both series of tests followed a common plan of daily bouts of aerobic work on motor-driven treadmills at a speed of 3.63 m.p.h. All running tests were conducted in the air-conditioned performance laboratory which provided a dry bulb temperature of 65°F and a 53% relative humidity. Noise, lighting and air movement were constant.

In the first series, performance was tested during a 40-minute period of standard treadmill running 1½, 4, 6 and 24 hours following the intake of 250 gm of commercial chow (Purina; 49% carbohydrate, 24% protein, 7% fat), completely consumed by 8:45 A.M. A fixed work intensity of 202.9 kg-m/min. was achieved for each dog by maintaining a constant treadmill speed and adjusting the grade between 9.4 and 12.5 degrees of inclination for differences in body weight. The animals were weighed after a 1-minute warm-up run which stimulated evacuation of the bowel and bladder.

In the second series, effect of carbohydrate and

Received for publication April 2, 1959.

[1] This paper reports research undertaken in cooperation with the Quartermaster Food and Container Institute for the Armed Forces, HQ, QM. Research and Engineering Command, U.S. Army, and has been assigned no. 979 in the series of papers approved for publication.

TABLE 1. *Characteristics of Treadmill Running at 3.63 m.p.h. and 10 Degrees of Inclination and Responses to Exhaustive Work in Six 8–12-Kg Dogs**

	cc/kg/min.
O_2 Uptake	58.0 ± 5.05
% Peak effort†	43.5 ± 4.57
Stride length, cm.	68.6 ± 1.16
Max. pulse rate/min.	249 ± 16.2
Max. rectal temp., °F	105.3 ± 0.85
Δ Blood glucose, mg. %	−30.0 ± 12.1
Δ Blood lactate, mg. %	+1.3 ± 1.0
Δ Venous O_2, cc/100 ml.	−0.5 ± 1.5
Δ Venous CO_2, cc/100 ml.	−6.4 ± 3.3

Values are means and S.D.s. * Measured in the post-absorptive state. † % Peak effort = observed O_2 uptake/max. O_2 uptake × 100.

TABLE 2. *Effect of Proximity of Mealtime on Physiologic Responses of Dogs to a 40-min. Treadmill Test (202.9) kg-m/min.)*

	Hours After Feeding			
	1½	4	6	24
Mean energy expenditure, cal/min.	3.36	3.52	3.52	3.31
Respiratory quotient	.93	.95	.91	.79*
Mean pulse rate/min.	216	223†	223†	211
Δ Rectal temp., °F	+0.9	+1.4‡	+1.6‡	+0.6
Tidal air, cc	245	263	238	222

Mean resting temperature was 101.2 ± .37°F. *Differs significantly from the 1½-, 4, and 6-hr. values, $P < .01$. †Differs significantly from the 1½- and 24-hr. values, $P < .01$. ‡Differs significantly from the 1½- and 24-hr. values, $P = .01$.

water supplementation on maximum aerobic work capacity in the post-absorptive state was determined, utilizing long-sustained, exhaustive running trials conducted at 10 degrees of inclination. Tests were conducted 17 hours after the last meal. The end point in exhaustive running was determined by failure of animals to maintain pace with the treadmill after six consecutive shocks from a 180-volt electric stimulator mounted at the rear of each treadmill. During the control phase of testing the dogs were run to exhaustion without benefit of supplementation. In the second trial, carbohydrate pellets in amounts equal to 0.5% of the body weight were administered orally following the drawing of the resting blood sample and 30 minutes prior to exhaustive running. The pellets had the following composition: sucrose 55%, dextrose 20%, dextrins 10%, starch 7% and water 8%. In the third trial, the dogs were permitted to drink distilled water ad libitum during the course of exhaustive running. For this purpose, watering pans were suspended from the sides of the treadmills to allow the animals to drink while in motion. Water intake was measured every 90 minutes.

Pulse rates were measured with a cardiotachometer; readings were taken every 5 minutes for the 40-minute trials and every 10 minutes during exhaustive running trials. Rectal temperature was taken with flexible thermistor probes, inserted 6 inches into the rectum, indicating through a multichannel telethermometer. Respiratory gas exchange was determined by collection in duplicate of expired air in chain-compensated gasometers and subsequent analysis of the samples for CO_2 and O_2; the exact details for these methods have been presented in previous papers by Young *et al.* (12a). For the 40-minute trials, expired air was collected at 19 minutes and 39 minutes after the start of running. Respiratory rate was determined from the number of deflections of a light-weight pen attached to the counter balance of the gasometer and recording on a kymograph drum. All respiratory measurements were converted to STPD volumes.

Resting and post-exercise blood samples were drawn from the radial vein; aliquots were set aside in heparinized capillary tubes for determination of hematocrit and the rest delivered into fluoridated tubes and immediately frozen for subsequent analyses for glucose (13), lactic acid (14) and acetone (15).

Characteristic responses to exhaustive running at 3.63 m.p.h. and 10 degrees of inclination are set forth in table 1.

RESULTS

Influence of Proximity of Last Meal on Economy of Work

Physiologic responses to work. Responses to the 40-minute standard work test at various times following a meal are set forth in table 2. Energy expenditure for the fixed work task was unaffected by proximity of the last meal. The mean energy expenditure was 3.43 Cal/min. with a standard deviation of ±0.51. Consequently, it follows that physical work efficiency was constant over the period tested. The respiratory quotient was reasonably constant at .93 up to 6 hours after feeding, indicating that during the first three periods following the intake of food, carbohydrate was the predominant fuel for muscular work. At 24 hours following the consumption of the meal, the respiratory quotient was lowered to .79. Tidal air was not affected systematically; the over-all ventilatory efficiency (cc O_2/l. air) was 15.9 ± 2.71.

Mean work pulse rate was highest at 4 and 6 hours after feeding. The mean pulse rate for these periods was 223/min. and significantly ($P < .01$) higher than that recorded at 1½ and 24 hours after feeding.

The average increase in body temperature due to work at 4 and 6 hours after feeding was +1.5°F, as compared with an average increase of +0.75°F at 1½ and 24 hours after feeding. The difference in the means is significant ($P = .01$).

Variation in body weight during the day. Variation in body weight during the day and following periods of work is a characteristic response in the dog. These data are set forth in figure 1. At 1½, 4, 6 and 24 hours after feeding the mean body weights of the test animals prior to work were 11.58 ± 1.03 kg, 11.83 ± 1.03 kg,

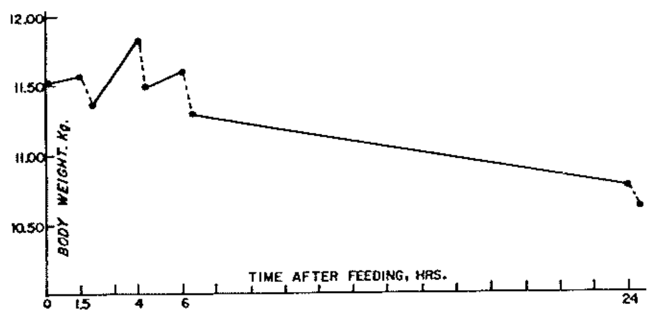

FIG. 1. Variations in mean body weight of 6 dogs following intake of 250 gm of commercial feed. Change in weight after a 40-min. treadmill test is indicated by *broken lines*. Body weight is shown on *ordinate*; time after feeding is shown on *abscissa*.

11.61 ± 0.85 kg and 10.77 ± 1.02 kg, respectively. The principal sources of variability in body weight during the test period were water loss during work and overcompensated fluid intake during rest periods. The state of hydration of the body must be related to these variations in weight. If it is assumed that the dog is in water balance (63 % body water) 6 hours after feeding and the variations in body weight observed at 4 and 24 hours following the meal are principally due to body water content, then the body water of an 11.61-kg dog at rest may be expected to vary from 65 % to 57 %. These possible differences in body water in our test animals are associated with a daily ad libitum water intake of 1229 ± 88 cc/dog.

Effect of Water and Carbohydrate Supplementation on Maximum Aerobic Work Capacity in the Post-Absorptive State

Determination of gross energy expenditure. Traditionally, gross work performance is expressed as energy expenditure. Within our experimental arrangements of studies of long-sustained endurance capacity, the total energy expenditure is usually determined from the mean rate of expenditure measured after 1 and 2 hours of running multiplied by the total running time. Reliability of this procedure may be inferred from the following example: during a 7-hour run to exhaustion at 3.63 m.p.h. and 10 degrees of inclination, the gross energy expenditure of a 10.37-kg dog has been computed to be 1332.2 ± 80.6 cal. This estimate is based on 14 measurements of respiratory gas exchange made every 30 minutes during the run. Gross expenditure computed from two measures of gas exchange is 1350.3 cal. The value obtained by the procedure of fewer measurements lies within one standard deviation of the mean shown during a single running trial, therefore, it is safe to assume that maximum work performance can be adequately determined from the product of the mean of two standard measures of respiratory gas exchange and total running time.

For a fixed grade and speed, maximum aerobic energy expenditure is reasonably constant despite variations in body weight and running time. On the basis of 30 long sustained running trials in six dogs, the mean gross caloric expenditure is 1193 cal. (S.E. of mean is ±28.2). However, since the rate of caloric expenditure is correlated with the body weight ($r = +.889$ [$P < .01$]), as is total running time ($r = +.655$ [$P < .01$]), steps were taken to insure constancy in the weights of the individual dogs for the sequence of tests by controlled feeding, in order to obviate any unusual bias referable to changes in body weight.

Corrections for changes in hematocrit. An increased hematocrit is a typical response to exhaustive work in the dog. The product-moment coefficient of correlation between increases in the hematocrit and variations in body weight during exhaustive running is −.947. Since the major portion of the body weight loss during work is due to water lost from the oral and respiratory surfaces, the correlation suggests a hemoconcentration through a reduction in plasma water. Further studies on blood volume and, in particular, red cell number and volume, are necessary to test this hypothesis.

The rationale for correcting blood values for differences in hematocrit arises from the fact that the 'apparent hemoconcentration' following exhaustive work varies with the dietary manipulations from little or no effect when water is offered to the post-absorptive animal during endurance testing to as high as +40 %, when the animal is run to exhaustion during starvation without the benefit of water. In the present series, the average increase in the post-exercise hematocrit was +20.9 %, +18.7 % and +3.2 % for the control, carbohydrate and water-supplemented trials, respectively. Accordingly, to eliminate changes in blood volume as a source of variability, the blood values have been corrected for differences in hematocrit after work.

Work capacity. Maximum endurance capacity and the effects of water and carbohydrate supplementation in six dogs are shown in table 3. The average maximum performance in the unsupplemented post-absorptive dog was 1191 cal. After the administration of carbohydrate, work capacity was not significantly affected. Provision of approximately 1.5 liters of water during work increased sustained endurance capacity to 2141 cal. This 79.8 % increase in working ability associated with water intake is highly significant ($P \ll .01$).

While provision of carbohydrate as fuel for the working muscles did not materially alter the capacity for sustained work, such treatment did result in improvements in both the respiratory quotient and post-exercise blood sugar. The mean R.Q. during both control and water-supplemented trials was .77; following the administration of carbohydrate the R.Q. was elevated to .85. The mean resting whole blood sugar over all trials was 79.0 ± 8.0 mg %. Following exhaustive running, the unsupplemented animals showed a mean fall of 39.3 mg % in the blood sugar, whereas for carbohydrate and water supplementation, the average decrease in the post-exercise blood sugar level was 20.2 and 14.5 mg %, respectively. Both water and carbohydrate supplementation served to minimize the fall in the post-exercise blood sugar. The average decrease in the blood

TABLE 3. *Effect of Water and Carbohydrate Supplementation on Maximum Aerobic Work Capacity*

	Supplement		
	None	Carbohydrate (52.4 ± 7.2 gm)	Water (1520 ± 172 cc)
	Trial No. 1	*Trial No. 2*	*Trial No. 3*
Max. work performance, Cal.	1191	1299	2141*
Respiratory quotient	.77	.85†	.77
Max. rectal temp., °F	105.4	105.7	104.2‡
Δ Blood glucose, mg %	−39.3§	−20.2	−14.5
Δ Blood lactate, mg %	−0.1	+0.8	−0.7
Δ Blood acetone, mg %	+0.9	+0.5	+1.3

Tests were conducted at 3.63 m.p.h. and 10 degrees of inclination. Values are means. *Differs significantly from both other treatments, $P < .01$. †Differs significantly from both other treatments, $P = .05$. ‡Differs significantly from both other treatments, $P < .10$. §Differs significantly from both other treatments, $P < .05$.

sugar in milligrams per cent per calorie expended during work was .033, .015 and .0067 for the control, carbohydrate and water supplemented trials, respectively. The dogs offered water ad libitum were capable of expending 842 cal. more than carbohydrate-supplemented dogs during exhaustive running, yet showed an essentially similar fall in the blood sugar. These results indicate that provision of water during work improves the mobilization and/or synthesis of blood glucose.

Blood lactic acid and acetone were unaffected.

Water loss during exhaustive work. Body water loss has been computed from the changes in body weight following exhaustive work. The percentage of change in body weight following exhaustive work was 11.2 ± 1.7, 11.1 ± 1.1 and 6.9 ± 0.77 for control, carbohydrate- and water-supplemented trials, respectively. The effect of water on minimizing weight loss during work is highly significant ($t = 5.5$; $P = .003$). Neglecting protein metabolism and utilizing the constants 4.1 and 9.3 as the caloric equivalents for 1 gm of body tissue carbohydrate and fat, respectively, a mean gross expenditure of 2141 cal. in the water-supplemented dogs at the observed R.Q.'s is associated with the combustion of approximately 119.0 gm of carbohydrate and 177.7 gm of fat. Since the animals showed a mean decrement of 724 gm in body weight during this trial, it is suggested that 427 gm were lost as water. By contrast, during the control phase of testing an expenditure of 1191 cal. is associated with the combustion of 98.9 gm of fat, 66.2 gm of carbohydrate and a loss of 1006 gm of water.

Final work body temperatures were related to the degree of dehydration. In the control series, 11.2% weight loss due to work was associated with a maximum rectal temperature of 105.5 ± 1.00°F. When water was provided during work, the average maximum body temperature attained was 104.2 ± 1.12°F. Probability of difference in the mean terminal temperatures lies between the 5% and 10% level of significance.

DISCUSSION AND CONCLUSIONS

Energy cost of performing a fixed work task (40–50% of peak effort) on the motor-driven treadmill is unaffected over a 24-hour period by the proximity of the last meal. The respiratory quotient tends to be higher in the first 6 hours after feeding, corresponding to the period of digestion and subsequent absorption of food. Twenty-four hours after feeding a respiratory quotient of .79 indicates a preponderance of fat and carbohydrate combustion.

Mean work-pulse rates, as well as the increases in rectal temperature due to work, show significant increases at 4 and 6 hours after feeding. These results indicate a slight loss in efficiency in cardiovascular performance and temperature regulation during work at 4 and 6 hours following a meal. Efficiency of the respiratory system as adjudged by the ventilatory efficiency during work is unrelated to the proximity of the meal.

While these experiments do not clearly rule out time of day as an important variable, our results on gas exchange are in good agreement with the recent report of Durnin and Namyslowski (15), who concluded that neither variations in time of day nor relatively light meals affected the energy cost for standardized tasks.

Probable diurnal variations in the body water content have been discussed. Following a standard work task, the dog tends to overcompensate in fluid intake to the extent of introducing considerable variability in the state of body hydration. Further studies of water metabolism in the working dog are required to more fully appraise these variations in body composition.

While provision of carbohydrate prior to work elevates the respiratory quotient and tends to minimize the fall in blood sugar, maximum aerobic work capacity is in fact unaffected by such supplementation. Our results are in marked contrast with those of Dill *et al.* (16), who found, on the one hand, a general relationship between running time in the dog and the depression in the blood sugar, i.e. the longer the running time the lower the blood sugar and, on the other hand, an increase in running time after the administration of glucose. These workers, however, confined their observation to one animal and do not provide sufficient data to permit an estimate of the reliability of their measures. The data presented here suggest that any real benefit on maximum work performance derived from supplementation with carbohydrate or simple sugars must lie in the process of recovery and preparation for subsequent work.

In contrast, the response to water supplementation is a marked improvement in endurance capacity. The factors which appear relevant are maintenance of the blood sugar level, a diminished degree of work dehydration and lower body temperatures. It is suggested that increased work capacity through water supplementation is mediated primarily by the maintenance of a relatively normal state of hydration and improvements in the temperature regulation and, secondarily, by a beneficial effect on carbohydrate metabolism.

In summary, it can be inferred from these experiments that there is a loss in economy of work at 4 and 6 hours following the intake of a substantial meal. While there is no measurable effect on calorie expenditure due to the specific dynamic action of the food, there is evidence of loss in efficiency in the cardiovascular system and in temperature regulation in the working dog. The practical implication of these changes is yet to be resolved. Data on the endurance component of fitness have been presented. Provision of water during exhaustive work performance markedly improves endurance capacity, whereas provision of easily utilizable sugars is without immediate benefit.

REFERENCES

1. Haldi, J. and W. Wynn. *Am. J. Physiol.* 145: 402, 1946.
2. Haldi, J. and W. Wynn. *J. Nutrition* 33: 287, 1947.
3. Haldi, J. and W. Wynn. *J. Nutrition* 31: 525, 1946.
4. Haldi, J., G. Bachmann, V. Enson and W. Wynn. *Am. J. Physiol.* 121: 123, 1938.
5. Carpenter, T. M. and E. L. Fox. *Arbeitsphysiologie* 4: 570, 1931.
6. Carpenter, T. M. and R. C. Lee. *Arbeitsphysiologie* 10: 172, 1938.
7. Wrightington, M. *J. Nutrition* 24: 307, 1942.
8. Daum, K., W. W. Tuttle, C. Martin and L. Myers. *J. Am. Dietet. A.* 26: 503, 1950.
9. Tuttle, W. W., K. Daum and B. Randall. *Fed. Proc.* 11: 164, 1950.
10. Haggard, H. W. and L. A. Greenberg. *Diet and Physical Efficiency.* New Haven: Yale Univ. Press, 1935.
11. Haggard, H. W. and L. A. Greenberg. *J. Am. Dietet. A.* 17: 753, 1941.
12. Nelson, N. *J. Biol. Chem.* 153: 375, 1944.

12a. Young, D. R., R. Mosher, P. Erve and H. Spector. *J. Appl. Physiol.* 14: 834, 839, 1959.

13. Barker, S. B. and W. H. Summerson. *J. Biol. Chem.* 138: 535, 1941.
14. Greenberg, L. A. and D. Lester. *J. Biol. Chem.* 154: 177, 1944.
15. Durnin, J. V. G. A. and L. Namyslowski. *J. Physiol.* 143: 573, 1958.
16. Dill, D. B., H. T. Edwards and J. H. Talbott. *J. Physiol.* 77: 49, 1932.