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Energy and electrolyte metabolism and adrenal responses during work in dogs¹

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YOUNG, D. R., R. PRICE, N. E. ELDER, AND R. R. ADACHI. *Energy and electrolyte metabolism and adrenal responses during work in dogs.* J. Appl. Physiol. 17(4): 669-674. 1962.—Studies with dogs were undertaken to determine whether nitrogen metabolism during aerobic treadmill running is affected by recency of food intake. Over a 6-hr period after intake of a standard meal, the percentage of energy derived from carbohydrate, fat, and protein oxidation was relatively constant at 70, 24, and 6, respectively. With postabsorptive dogs, the percentages of energy derived from carbohydrate, fat, and protein were significantly different ($P < .01$) and in the ratio of 45:53:2. Urinary nitrogen, amino acids, 17-hydroxycorticosteroids, Na, and K were examined in postabsorptive animals at rest and at work. Over a 3-hr period, the urinary NPN and Na were 0.49 g and 5.8 mEq, respectively, and unaffected by work; K and hydroxycorticosteroids were 4.6 mEq and 228 μ g, respectively, and significantly elevated during work. Of 18 amino acids measured, only cystathionine excretion was significantly altered during work. In running trials of 88-600 min duration, both NPN and 17-hydroxycorticosteroids showed a tendency to increase with caloric expenditure.

IN AN EARLIER STUDY with postabsorptive dogs (1), we measured the urinary nitrogen during controlled levels of aerobic work. On the basis of these studies, which applied the classic methods of indirect calorimetry, we estimated the percentage of calories derived from the direct oxidation of carbohydrate, fat, and protein to be relatively constant and in the ratio of 65:32:3. Preliminary comparisons of the responses measured during physical activity and at rest suggested a protein-sparing effect of work. Thus, over a 24-hr period of rest with an average energy expenditure of 700 kcal, the dogs excreted 2.19 g of nitrogen; during work of comparable caloric cost, the nitrogen excreted was 0.53 g.

Additional studies have been undertaken to evaluate

energy and nitrogen metabolism at rest and during work. Investigations have been carried out with fed and with postabsorptive dogs. In order to assess the influence of the adrenal glands, measurements have been made of the urinary excretion of corticosteroids, norepinephrine, and electrolytes.

METHODS

The animals used were well-conditioned male beagle dogs weighing 8-12 kg. The series of tests required approximately 1 year for completion; the average age of the animals was 42 months. Body weights were held constant throughout the entire period by controlled feeding (Purina chow). All tests were conducted in an air-conditioned laboratory which provided a dry-bulb temperature of 18.0 ± 1.6 C and a relative humidity of $41\% \pm 15$. Noise, lighting, and air movement were constant.

The data presented have been drawn from three major studies. In the first series, energy metabolism was examined in seven dogs during work at 2, 6, or 17 hr after the intake of a standard meal; the caloric expenditure during work was similar to the energy contained in the food consumed (670 kcal). In the second series, seven postabsorptive dogs were used to study metabolism during one period of work (3 hr, 600 kcal) and two periods of rest (3 hr, 68 kcal; 24 hr, 670 kcal). Finally, metabolism was examined in five postabsorptive dogs in work tests of 88-600 min duration where total energy expenditure varied from 300 to 1800 kcal. Within each series, the tests were administered in a random order. All studies of the postabsorptive state were initiated 17 hr after the last feeding.

For 24-hr resting measurements, the dogs were placed individually in standard stainless steel metabolism cages and the urine was collected under toluene in narrow-mouthed polyethylene bottles. Daily energy expenditure of the caged dogs was inferred from the results of several feeding studies and varied between 600 and 800 kcal, Table 1.

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TABLE 1. Daily food and water intake and variations in body weight in 8-12-kg dogs

	24-Hr Rest
Food intake, kcal*	670±48.5
Water intake, ml	547±44.6
Δ Body weight, g	+16±6.0

Values are means ± SD. * Purina chow.

During the 3-hr resting tests, energy metabolism was determined by collection of a series of 10-min samples of expired air while the animals were lying quietly on a table. For this purpose, the dogs were fitted with a tight-fitting mask permitting only nasal breathing through a double Douglas valve. Expired air was collected in a spirometer and analyzed for CO₂ and O₂ content with a Haldane apparatus and Beckman oxygen analyzer, respectively. Prior to actual testing, the dogs were catheterized; their bladders were drained and rinsed with 20 ml of isotonic glucose. After the period of observation, urine was obtained by the same technique.

All work tests followed a common plan of aerobic work on treadmills driven at a speed of 3.63 mph. The grades were adjusted to provide a constant workload of 202.9 kg-m/min. The tests were initiated after emptying of the bladder. During work, urine was collected with a plastic collecting device described elsewhere (1) and also by catheterization. Gas exchange and energy

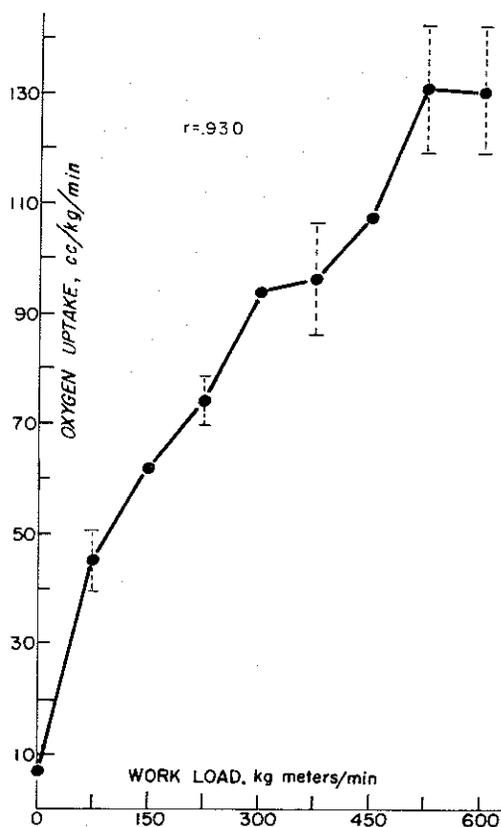


FIG. 1. Oxygen uptake in relationship to workload in 8-12-kg dogs.

expenditure were determined by using specially constructed masks which permitted opening of the mouth and panting; a series of 2-min samples of expired air was collected in chain-compensated gasometers beginning 30 min after the start of running until the termination of work. The relationship between work load and oxygen uptake is shown in Fig. 1. More basic studies of respiratory gas exchange in relationship to work have been presented earlier (2).

After urine volume was measured, all samples were frozen for subsequent analyses. Nonprotein nitrogen (NPN) was determined by the micro-Kjeldahl method after treatment of the urine with cold trichloroacetic acid. Ammonia, taurine, and amino acids were determined in unhydrolyzed urine samples with the Phoenix amino acid analyzer (3, 4). Urinary sodium and potassium were determined with the Coleman model 21 flame photometer. Urinary 17-hydroxycorticosteroids (17-OHCS) were determined spectrophotometrically (5) after incubation of the samples for 30 hr at 37 C with β-glucuronidase (6). Catecholamines, expressed as norepinephrine (NE), were determined by a fluorometric method (7, 8). For the latter two determinations, only the purest grade reagents were used.

The animals were allowed free access to water throughout the tests, and records were kept of the fluid intake and changes in body weight. Metabolized energy was calculated from the respiratory gas exchange and nitrogen excretion by means of the equations of Newburgh et al. (9). The reliability of values thus obtained has been discussed previously (1).

RESULTS

Food intake and metabolism during work. Energy metabolism was examined in seven dogs during work after the intake of a standard meal known to maintain daily weight balance. Theoretical considerations, notably the relationship between energy balance and nitrogen excretion, suggested that the most favorable comparisons are obtained from tests where intake and expenditure are similar. Note in Table 2 that during work at 2 hr or 6 hr after intake of 670 kcal, the percentage of calories derived from carbohydrate, fat, and protein oxidation is relatively constant at 70, 24, and 6, respectively.

TABLE 2. Energy derived from carbohydrate, fat, and protein during work in 7 dogs after a standard meal (670 ± 48.5 kcal)

	W ₂ * (634 kcal)	W ₆ * (576 kcal)	W ₁₇ * (600 kcal)
RQ	.90±.08	.92±.06	.84±.05
Calories from CHO, %	69.9±17.1	69.4±10.4	45.1±16.4†
Calories from fat, %	23.8±17.3	23.5±9.84	52.7±16.2†
Calories from protein, %	6.35±1.48	7.06±2.16	2.29±0.59†

Values are means ± SD. * Work at 2, 6, or 17 hr after food intake (Purina chow). † Significantly different from values at 2 or 6 hr after feeding, $P < .01$.

TABLE 3. Gross energy expenditure and urinary excretion of nitrogen, electrolytes, 17-hydroxycorticosteroids, and norepinephrine in 7 postabsorptive dogs

Physical Activity	Energy Expend., kcal	NPN		Na		K		17-OHCS, μ g	NE, μ g
		Total g	mg/min	Total mEq	mEq/min	Total mEq	mEq/min		
Rest, 24 hr	600-800	2.09 \pm 0.59	1.4 \pm 0.42	16.3 \pm 5.9	0.011 \pm 0.004	10.4 \pm 2.5	0.007 \pm 0.001	618 \pm 300	28 \pm 7.4
Rest, 3 hr	67.9 \pm 14.6	0.50 \pm 0.13	2.8 \pm 0.72	3.9 \pm 2.0	0.022 \pm 0.011	1.6 \pm 0.65	0.009 \pm 0.003	98 \pm 17	
Run, 3.05 \pm 0.39 hr	600	0.49 \pm 0.13	2.7 \pm 0.90	5.8 \pm 2.9	0.032 \pm 0.018	4.6 \pm 2.1*	0.026 \pm 0.012	228 \pm 86†	3.7 \pm 1.7

Values are means \pm SD. * < Significantly different from values obtained during 3-hr rest, $P < .05$. † Significantly different from values obtained during 3-hr rest, $P < .01$.

Seventeen hours after feeding, the percentages of energy derived from carbohydrate, fat, and protein were significantly different ($P < .01$) and in the ratio of 45:53:2.

The percentage of utilizable energy in the food derived from carbohydrate, fat, and protein was calculated to be 53, 19, and 29, respectively. The substrates oxidized during work, particularly protein, are quantitatively different from the calories consumed.

Additional investigations were undertaken to determine the influence of physiologic factors associated with work on the respiratory quotient. In a previous paper (10), we reported a rapid rise in body temperature during work performed at 4 hr or 6 hr after feeding. Associated with elevated body temperature there was a slightly elevated RQ and a 6% increase in energy cost during work. The product-moment coefficient of correlation, based on 52 separate running trials, between RQ and body temperature (101.6-104.6 F) is +0.580 ($P < .01$). Thus, 34% of the variability in the respiratory quotient is associated with variations in body temperature. Relatively minor differences in RQ alter markedly the results of metabolic calculations, and it is possible that the variations indicated in Table 2 are associated to some extent with temperature regulation.

Metabolism at rest and during work. Gross energy expenditure and the urinary excretion of NPN, Na, K, 17-OHCS, and NE were measured in seven postabsorptive dogs at rest and during work. These data are shown in Table 3.

Comparisons have been made of the results obtained for the two periods of rest. The average 24-hr excretion of Na, K, and 17-OHCS was 16.3 mEq, 10.4 mEq, and 618 μ g, respectively, and, as to be expected, was approximately eight times greater than values obtained during the 3-hr rest period. Small sample size prevented determination of urinary NE during the 3-hr period of rest. The 24-hr excretion of nitrogen was 2.09 g and only four times greater than measured values during the 3-hr trial. Replicated measures of daily nitrogen excretion in caged dogs showed good agreement (2.28, 1.95, 2.19, and 2.09 g), and additional catheterization at the termination of the test period did not reveal any further increase in the daily level measured. It is possible that the relatively low values for nitrogen reported here are

associated with loss of volatiles from the urine collecting pans. Indeed, this is suggested by the data for excreted ammonia, presented subsequently.

Comparisons have been made of urinary excretion during the 3-hr periods of work and rest. During treadmill running, the urinary NPN and Na were 0.49 g and 5.8 mEq, respectively, and were unaffected by work. On the other hand, urinary K and 17-OHCS were 4.6 mEq and 228 μ g, respectively, and were significantly elevated during work.

TABLE 4. Urinary excretion (in μ moles) of ammonia, taurine, and amino acids in postabsorptive dogs

	Physical Activity		
	Rest, 24 hr	Rest, 3 hr	Work, 3.05 \pm 0.39 hr
	<i>Acidic and Neutral</i>		
Taurine	611 (1030-242)*	55.7 (177-5.5)	129 (198-85)†
Asparagine and glutamic acid	50.4 (81.0-32.8)*	13.1 (22.1-5.9)	14.5 (19.0-12.5)
Serine	45.0 (65.2-27.9)*	6.1 (9.7-3.3)	8.2 (11.9-5.1)
Alanine	32.2 (72.8-23.5)*	8.2 (11.7-3.9)	8.4 (12.4-3.9)
Glycine	25.4 (50.2-4.1)*	3.9 (7.0-1.8)	5.4 (7.5-3.1)
Threonine	26.3 (45.8-19.6)*	5.2 (9.9-2.6)	5.7 (8.9-2.1)
Aspartic acid	14.5 (27.0-4.5)*		2.2 (2.4-1.8)
Glutamic acid	12.8 (17.8-6.9)*		2.7 (3.4-2.2)
Isoleucine	10.6 (21.7-3.6)*	2.6 (4.8-1.0)	4.2 (5.2-3.4)
Cystathionine	9.5 (14.2-6.0)*	9.0 (12.1-6.5)	3.2 (3.6-2.2)†
Methionine	9.3 (13.0-4.6)*	2.4 (3.4-1.4)	2.9 (9.0-2.2)
	<i>Basic</i>		
Ammonia	1010 (2410-519)*	282 (532-127)	362 (465-239)
1-Methylhistidine	99.4 (153-63.4)*	15.0 (27.9-8.2)	20.3 (24.9-12.0)
3-Methylhistidine	32.9 (47.2-21.1)*	5.1 (6.7-3.0)	4.8 (10.0-2.2)
Ethanolamine	14.5 (28.5-9.0)*	Trace	3.8 (6.4-1.2)
Lysine	13.5 (22.1-4.2)*	2.9 (4.3-1.3)	3.2 (4.2-1.6)
Histidine	12.4 (17.1-4.9)*	Trace	2.5 (2.8-0.0)
Tryptophan	11.9 (17.5-7.7)*	Trace	3.6 (5.7-1.5)
Ornithine	6.7 (18.4-2.7)	Trace	Trace

Range of values in parentheses. * 24-hr rest values are significantly higher than 3.05-hr work values, $P < .05$. † 3.05-hr work values are significantly different from 3-hr rest values, $P < .05$.

Finally, comparisons were made of urinary excretion during periods of comparable energy expenditure (rest 24 hr and run 3.05 hr). The excretion of nitrogen, Na, K, 17-OHCS, and NE was consistently higher at rest than during the period of work.

The excretion of ammonia, taurine, and 18 amino acids is shown in Table 4. In addition to these, we have noted the presence of undetermined polypeptides and traces of valine, cystine, leucine, tyrosine, phenylalanine, and aminoisobutyric acid. All values measured during the 24-hr period of rest were six to eight times higher than those obtained during the 3-hr trials. Ammonia, which was the largest single component measured, was not as high in the 24-hr samples as anticipated, thus suggesting some loss as a result of the collection technique. The only significant effect attributable to work was an increase in taurine and reduction in cystathionine excretion. However, the physiologic significance of these differences is obscure.

Effect of work period. Nitrogen, 17-OHCS, and NE excretion were studied in five postabsorptive dogs during four controlled levels of work: 300, 600, 1200, and 1800 kcal (see Table 5). In general, urinary volume, nitrogen, and 17-OHCS increased with energy expenditure.

TABLE 5. Urinary excretion of nitrogen, 17-OHCS, and norepinephrine during work in 5 postabsorptive dogs

	Energy Expenditure, kcal			
	300	600	1200	1800
Urine vol., ml	70±15	75±24	122±28	150±52
NPN, g	0.59±0.44	0.53±0.14	1.29±0.54	1.89±0.59
17-OHCS, µg	173±46	236±58	481±123	636±176
NE, µg	10±6	16±4	24±13	22±4

Values are means ± SD.

Correlations between 17-OHCS and nitrogen excretion, urinary volume, running time, and energy expenditure are shown in Table 6. Average NPN excreted varied between 0.59 and 1.89 g and was related to energy expenditure and running time; the product-moment coefficient of correlation between NPN and these two functions is +0.778 and +0.675, respectively. The partial correlation, removing the influence of running time, between NPN and work energy is +0.775, indicating that approximately 60% of the variations in nitrogen excretion are associated with energy expenditure per se. Average urinary 17-OHCS varied from 173 to 636 µg. The partial correlation coefficient between 17-OHCS and energy expenditure is +0.710; thus 50% of the variations in 17-OHCS are associated directly with work energy.

TABLE 6. Correlations between energy expenditure, running time, urinary volume, nitrogen, and 17-OHCS during work

Work energy × run time	.979
NPN × work energy	.778
NPN × run time	.675
NPN × work energy	.775*
17-OHCS × urine volume	.919
17-OHCS × work energy	.830
Urine volume × work energy	.677
17-OHCS × work energy	.710†

* Partial correlation (independent of run time). † Partial correlation (independent of urine volume).

Average NE excretion varied from 10 to 24 µg over all of the running trials. The product-moment coefficient of correlation between NE and energy expenditure is 0.02; therefore, there is no evidence that urinary NE is related to energy metabolism during work.

DISCUSSION AND CONCLUSIONS

Energy metabolism has been examined in the dog in relationship to food intake and physical work. In the postabsorptive state, the mean RQ during work was .84, or approximately 6% lower than values reported previously for dogs (1). The present results indicate that the calories derived from the oxidation of carbohydrate, fat, and protein are in the ratio of 45:53:2%. Comparable ratios have been obtained in tests with human subjects. We calculated energy metabolism from the recent studies of Johnson and Passmore (11); on the basis of the results reported for eight 2.5-hr periods of treadmill walking (850/kcal) with their subject RP, we calculated the energy derived from carbohydrate, fat, and protein to be 31, 65, and 4%, respectively. Earlier studies by Benedict and Cathcart (12) suggest an even higher level of carbohydrate oxidation during work. During the 4-hr, 22-min "century run" on a stationary bicycle, they measured consistent work RQ's of .91, which indicates that approximately 70% of the calories were derived from carbohydrate.

Over a 6-hr period after the intake of food, the percentages of energy expended during work derived from carbohydrate, fat, and protein are 70, 24, and 6, respectively. Thus, feeding a meal relatively high in carbohydrate and protein increases carbohydrate and protein oxidation and reduces fat oxidation. Although metabolism during work is undoubtedly influenced by food intake, our data indicate that the fraction of energy derived from the oxidation of carbohydrate, fat, and protein differs from the distribution of energy in the food consumed.

We have never measured a large increase in oxygen uptake during work referable to the specific dynamic action of protein. In an earlier study (10) and in the present series we observed increases of 3-6% in the rate of energy expenditure during treadmill running at 6 hr after feeding. Since these variations are within the range

of experimental error, we have considered them to be of relatively minor importance. However, the magnitude of change is similar to that observed by Orr and Kinloch (13). These workers found a 2.5% increase in energy metabolism in a marching subject after intake of 100 g of plasmon (80% casein). Although preliminary investigations indicate a relationship between body temperature and RQ, it is felt that the error in the metabolic calculations introduced by variations in temperature would be minor. Nevertheless, additional studies in this area are desirable.

In postabsorptive dogs, the nitrogen excreted is unaffected by 3-hr periods of work. Accordingly, it is suggested that during moderate work, the urinary NPN is largely a function of time and is unrelated to energy expenditure. During long-sustained work, however, there is a tendency for the NPN to rise in direct relationship with energy expenditure. Earlier findings show a direct effect of the adrenal cortical steroids on nitrogen excretion. Long et al. (14) found that administration of cortical extract increased nitrogen excretion and the level of blood glucose in the adrenalectomized rat. Our present findings are not in accord with the hypothesis that the hormones of the cortex accelerate urinary nitrogen elimination. For example, during the 3-hr running trials, urinary 17-OHCS was approximately doubled, indicating a significant increase in cortical activity; nevertheless, the nitrogen excreted was unaffected. For longer periods of work, urinary 17-OHCS was associated with energy expenditure and thus to nitrogen excreted. However, a stronger relationship was established between 17-OHCS and urine volume ($r = +0.919$), and therefore it is suggested that urinary 17-OHCS is more closely associated with water metabolism than to nitrogen metabolism.

Additional tests were undertaken to study urinary 17-OHCS and nitrogen during work at 2 hr and 6 hr after feeding. However, due to the presence of hydrocortisone-like substances in the food consumed and the excretion of relatively large amounts of 17-OHCS, the results were unclear. On the basis of studies with hot-water extracts of homogenized samples of feed, we estimate the steroid content of the food to be 8 $\mu\text{g/g}$ dry weight.

Urinary excretion of catecholamines was variable. During one series of treadmill tests (600 kcal), average excretion of norepinephrine was 3.7 μg . In a second test, excretion of norepinephrine was 16 μg , and statistical analysis did not show a systematic relationship between energy expenditure and urinary catecholamines. In view of the variability and the reported metabolism of sympathomimetic amines by body tissues (15-17), it is

felt that further tests along these lines would be unrewarding.

The daily excretion of Na and K presented above is essentially similar to values reported for dogs elsewhere (18). The excretion of K was elevated during work; Na was unaffected.

In previous reports we presented evidence to support the concept of gluconeogenesis during work in the dog. With postabsorptive animals (19), we found a tendency for the blood sugar level to decline during the early phases of exhaustive running and then to rise during the late stages of work. Perhaps the most dramatic increase in blood sugar was observed in one dog during a 5-day period of food deprivation (20). After 38.7 hr of continuous running, the blood sugar was 28 mg/100 ml higher than the level measured immediately prior to work. In the present series, we examined energy metabolism during long-sustained work tests in which, theoretically, the preformed stores of carbohydrate should have been depleted. Nevertheless, the metabolic data presented in part elsewhere (1) indicated a consistently high level of carbohydrate oxidation during work, and preliminary calculations suggested that approximately 360 g of carbohydrate was derived from the body fat. We have disregarded protein as a major source of fuel, since in the postabsorptive animal it provides only 2-3% of the total required energy; in the fed animal, protein oxidation provides at best 7% of the total energy expended during work. Further, the amount of protein involved could contribute only slightly to gluconeogenesis. For example, during the longest running trials, average urinary nitrogen was 1.89 g. Neglecting the excretion of amino acids, urea, etc., and assuming that the nonnitrogenous moiety of protein is converted quantitatively to carbohydrate, no more than 10 g (40 kcal) of carbohydrate could be derived from protein.

The present results reaffirm our belief that substantial amounts of carbohydrate may be derived from the body lipids; this is not in accord with the apparently impressive earlier studies supporting the Hill-Meyerhof theory of preformed carbohydrate utilization during muscular work. Our hypothesis is supported by the results of recent research with human subjects. In a study of the effect of calorie insufficiency, Vaughan et al. (21) concluded that "overweight" subjects were able to maintain higher blood sugar levels throughout periods of semistarvation while excreting significantly less ketones. There was also a tendency toward a reduction in urinary nitrogen. These findings led the authors to postulate an increased production of sugar from fat, a conclusion similar to our own.

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