

A COMPARISON OF OXYGEN CONSUMPTION IN NORMAL
AND EXPERIMENTALLY DEHYDRATED RATS

by

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INTRODUCTION

Several studies have been made concerning the effects of stress on the thyroid gland. It is generally agreed that, except for certain special cases, thyroid activity is inhibited by a wide variety of chemical, physical, and emotional stressors. However, little work has been done using dehydration as the stressor agent. Results of these few studies are contradictory.

The method commonly used for assessing the metabolic activity of an animal is the determination of the rate of oxygen consumption. Few studies have employed the measurement of oxygen consumption as an index of body metabolism during stress.

The purpose of this study was to compare the oxygen consumption over a period of days of normal white rats with that of white rats subjected to experimental dehydration.

REVIEW OF LITERATURE

Selye (1936) described the general adaptation syndrome in rats that had been subjected to a variety of physical and emotional stressors. Bogorech (1951) observed that rats subjected to forced muscular exercise, subcutaneous injections of formalin, or spinal cord transection showed a decreased rate of radioiodine pickup by the thyroid gland. It was concluded that thyroid gland activity was depressed.

Both frequent housing changes and forced muscular exercise were seen by Carriere (1959) to prevent the thyroid hypertrophy resulting from iodine deficiency in mice. Since control animals fed a low iodine

diet displayed thyroid stimulation, it was concluded that these stressors depressed thyroid activity.

Sackler (1959) observed a more dense thyroid colloid in rats subjected to intense auditory stress than in controls. He feels this may indicate increased colloid storage as a result of alterations in the release mechanisms of the thyroid gland.

Stress in rabbits produced by electrical shock, restraint, abrupt lighting changes, surgery, or injection of turpentine induces a prompt inhibition of one or two days duration in the release of I^{131} -labeled hormone from the thyroid gland (Brown-Grand, et. al., 1954). Rats, according to van Middleworth (1951), when fed a low iodine diet and subjected to surgical trauma, severe intestinal injury, or starvation, displayed a decreased uptake of I^{131} by the thyroid gland and a reduced labeling of plasma PBI by the radioiodine. It was concluded that thyroid activity was depressed.

Paschkis, et. al. (1950) used intramuscular injections of ten per cent formalin to induce stress in rats. The decreased rate of uptake of radioiodine by the thyroid gland was taken as an indication of thyroid inhibition. Working with rabbits anesthetized with urethane, Mollur (1935) showed that injection of NaCN produced an immediate initial rise in oxygen consumption, followed quickly by a marked decrease. Pinter (1952) has shown that the subcutaneous injection of aminothiazole decreases oxygen consumption in the rat.

The histological picture associated with low thyroid activity was observed by Schmidt (1938) in both male and female guinea pigs that had been subjected to heat at 32°C . and a high humidity for two to six weeks.

Pipes, et. al. (1960) subjected adult female Swiss Webster mice to underfeeding. The thyroxine secretion rate decreased progressively as the food consumption decreased. Craven (1951) fed young male rats a diet of raw carrots and tap water ad libitum for ten days. At the end of this period of partial inanition the oxygen consumption of these rats was twenty per cent below that of the previously established normal levels. Meites and Wolternik (1950) have shown that severe starvation in rats greatly decreases the thyroidal uptake of radioiodine. Mulinos and Pomerantz (1940) previously reported similar findings. They attributed the depression of thyroid activity to a decrease in thyrotropic function by the pituitary gland. Water deprivation has been shown by Reichlin (1957) to induce a progressive decrease in the release rate of I^{131} from the thyroid in rats. It was concluded that the level of food intake was the major factor in determining thyroid activity regardless of the degree of dehydration.

Other workers have reported evidences of increased thyroid activity in response to a variety of stressor agents:

Selye (1936) observed thyroid inhibition during the early stages of the resistance of rats and guinea pigs to stress. However, during the second stage of resistance (beginning approximately 48 hours after injury) the thyroid showed a tendency toward hyperplasia.

It is generally agreed that exposure to cold stimulates thyroid activity. Hale, et. al. (1959) have shown that cold exposure in rats produces histological conditions in the thyroid typically associated with high activity levels. Rats maintained at $5 \pm 1^{\circ}\text{C}$. by Woods (1956) had a greatly increased thyroxine secretion rate after two weeks. Hsieh (1957) has shown that rats exposed to cold responded by a definite

increase in oxygen consumption; this response persisted after thyroxine stores had been depleted. It was concluded that the metabolic response to cold is not directly dependent upon the amount of circulating hormone.

Mice kept in continuous light for 28 days by Puntriand (1951) displayed reduced thyroid weights and reduced thyroidal uptake of radioiodine, whereas, continuous darkness resulted in both increased thyroid weights and uptake of radioiodine. It was concluded that continuous light depressed thyroid activity and continuous darkness resulted in thyroid stimulation.

Smith, et. al. (1951) have shown that rats subjected to X-ray irradiation and starvation maintained a higher oxygen consumption level than did their starved controls. Oxygen consumption measurements were taken daily; all animals were dead by day eight. Vacek (1960) has also observed increased oxygen consumption in rats subjected to irradiation.

Rats given subcutaneous histamine injections were shown by Gyernek (1950) to increase oxygen consumption in an environmental temperature of 30°C. Rats given DDT by incorporation into their diet showed increased oxygen consumption, as judged by excised liver slices, over that of controls (Jandorf, et. al., 1946). No change in oxygen consumption was noted when DDT was administered by stomach tube daily for from 30 to 50 days.

Gerwing (1958) used twice-weekly injections of Clostridium septicum toxin as a stressor agent in rats and guinea pigs. The release rate of I^{131} from the thyroid gland was depressed primarily, then rose to normal after about ten days, and terminated in a phase of above normal secretion rates. It was concluded that this long term stress stimulated thyroid activity. Brand (1951) observed that rats infected with

Trypanosoma equiperdum or Trypanosoma evansi displayed a significant increase in oxygen consumption only during the 36 hours immediately preceding death. The increase in oxygen consumption was only in part due to increased oxygen use by the infecting organisms.

Swartz (1960) found that dehydration in rats brought a lowered FBI level during the first four days. However, FBI levels increased from the fourth to the sixth day; after day six the levels dropped back to below normal. The thyroid cuboidal epithelium showed a small but significant increase in height over the controls after two days dehydration. This increase in epithelial cell height progressed as the dehydration period continued.

Hertzel, et. al. (1952) found stimulation of thyroid activity in humans which had undergone, or were undergoing, stressful situations. Volpe, et. al. (1960), however, observed no significant alteration of serum FBI concentrations of various human groups while being subjected to the stresses and strains of examination, athletic contests, major surgical procedures, or myocardial infarcts.

METHODS AND MATERIALS

Fifty rats (35 males and 15 females) of the Sprague-Dawley strain, weighing between 235-380 grams, were used. For each experiment except one (Expt. V) the test and control groups were of the same sex. The animals were housed in groups of five each in cages measuring 2 feet by 1.5 feet by 1 foot. Purina lab chow and tapwater were fed ad libitum. Dyes were used to mark each animal for individual recognition. Body weights for all animals were recorded prior to each daily measurement

of oxygen consumption.

The rats were allowed to recover from shipment for several days. Then each animal was placed in the oxygen measurement apparatus two hours daily for five or six days in order to acclimatize it to these conditions before beginning oxygen consumption determinations.

Oxygen consumption determinations were made for a period of one hour on consecutive days. Each rat was given three daily trials while on food and water ad libitum in order to establish a base level of oxygen consumption. The water bottles were then removed from those animals selected for dehydration. Oxygen consumption determinations for the dehydrates and watered controls were then continued for seven to nine, usually eight, days. The animals were then killed by an overdose of ether. Thyroid and adrenal tissues were removed and placed in Bouin's fluid. No use has as yet been made of these tissues in this study.

A sequence of 10 experiments was carried out during this study. Excessive activity of the animals during certain of the experiments caused the data from these experiments to be of questionable value. Six experiments will be discussed here.

Experiments I and II were pilot runs with each using a single group of female rats; limitation of time and equipment precluded the testing of more than one group per day. The weight ranges for animals in experiments I and II, respectively, were 246-284 grams and 235-274 grams. After establishing base level values for oxygen consumption, dehydration and oxygen consumption measurements were continued for seven days in experiment I and for eight days in experiment II.

Experiment III consisted of ten male rats ranging in weight from

240-283 grams. They were divided into two random groups of five each. After base level values were established, one group was dehydrated and tested daily for seven days. The watered control group was tested for eight days.

Experiment IV was a repetition of experiment III, except that an older group of male rats was used. The weight range was 263-341 grams. Oxygen consumption trials were carried out for eight days on both groups.

Experiment V was also a repetition of experiment III except that a group of five females, rather than males, was used as the watered controls. The females ranged in weight from 277-288 grams and the males from 323-378 grams. After establishing base level values for oxygen consumption, both the dehydrated males and the watered females were tested for nine days.

Experiment VI was also a repetition of experiment III. These male rats ranged in weight from 240-261 grams. Both the dehydrates and controls were tested for eight days. The dehydrated group showed excessive activity during the later test periods. These data are considered to be of little or no value.

The oxygen measurement apparatus consisted of: (1) a livestock watering tank, measuring 4 feet by 2 feet by 2 feet, used to contain a constant temperature water bath and fitted with a stirrer, a thermometer, a platform for holding the reaction flasks, and side brackets for supporting a series of manometers; (2) a series of five chemical dessicators (250 mm. inside diameter) with a net volume of approximately 8860 cc. each, used as reaction flasks; and (3) a series of five manometers with the necessary tubing (Plate I). Brodie's fluid was used in

EXPLANATION OF PLATE I.

A photograph of the apparatus used for the measurement of oxygen consumption. During operation each reaction flask is submerged in the water bath and connected with rubber tubing to one of the manometers.

PLATE I



the manometers. Each reaction flask was fitted with fifteen pounds of lead ballast to keep the flask entirely submerged, a pan to hold 150 grams of sodalime used as carbon dioxide gas absorbent, and a wire platform to hold the test animal (Plate II). The sodalime (Dewey and Almy Sodasorb, high moisture type 14-19 per cent, mesh size 4-8 Tyler, 4-8 "USS") was renewed after each trial. The water bath was kept at a temperature of $19 \pm 0.5^{\circ}\text{C}.$, and the room temperature at $22 \pm 2^{\circ}\text{C}.$

Measurements of relative oxygen consumption were made by recording the number of millimeters which the manometer fluid rose as a result of the pressure decrease within the system caused by inhalation of oxygen by the rat and absorption by the sodalime of exhaled carbon dioxide. When the column of manometer fluid had risen 40 to 50 millimeters the system was opened to allow the fluid level and system pressure to return quickly to normal. The system was then immediately closed and the fluid level allowed to rise once more. The manometer fluid column was allowed to rise only 40 to 50 millimeters so as to minimize any effect that the weight of the column may have had on the accuracy of the readings taken. A thermobarometer was used to correct for any pressure fluctuations due to atmospheric or temperature changes.

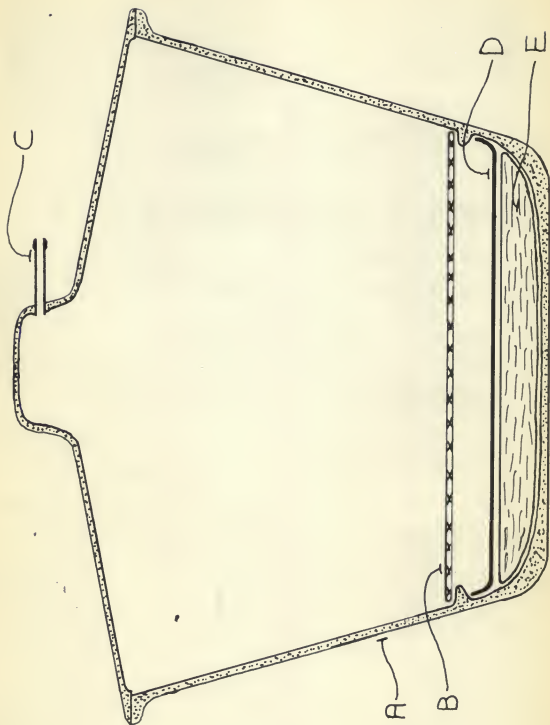
Since the volumes of the reaction flasks varied slightly from one another each animal was rotated daily among the flasks according to a set pattern. A time interval of 20 minutes was always observed after introducing the rat and flask into the water bath and before measurement began. This was thought necessary both to insure temperature equilibrium between the flask and water bath and to allow time for the animals to become settled. All measurement trials were carried out between 10 a.m. and 4 p.m. which, according to Horst and Mendel (1934),

EXPLANATION OF PLATE II.

A schematic drawing in cross section of a chemical dessicator fitted for use as a reaction flask.

- A. Dessicator.
- B. Mesh wire platform for supporting the test animal.
- C. Outlet leading to the manometer.
- D. Pan used to contain sodalime absorbent.
- E. Lead ballast.

PLATE II.



marks the physiological low period for the white rat. Each group of five test animals was tested at or very near the same time each day.

The only additional oxygen given an animal during the test period was that small amount introduced when the system was opened periodically to return the pressure and fluid level to normal. The rats gave no indication of anoxia. Krantz and Carr (1935) gave an average oxygen consumption rate for rats of 185 mg /100 gms. of body weight per hour. Using this figure, and assuming an atmospheric oxygen concentration of at least 20 per cent, a 380 gram rat would consume approximately 40 per cent of the originally available oxygen supply. The reaction flask oxygen concentration would not be reduced to below 12 per cent.

Rudolph and Puchstein (1955) stated that only after a certain latent period did the gradual diminution of oxygen concentration to 12 per cent cause a drop in body temperature and oxygen consumption in rats. The length of this latent period was not available. In the present study a cross-section of the larger oxygen consumption values was analyzed. Fluid column movement in millimeters was plotted against time in minutes. No appreciable decrease in the rate of oxygen uptake was seen to occur during the later stages of the test period.

EXPERIMENTAL RESULTS

Oxygen Consumption

All oxygen consumption values are expressed here as per cent of the base level values which were determined for each group prior to the beginning of testing.

Oxygen consumption decreased rapidly during the first three days of dehydration (Table I). From day four through day six of dehydration the rate of decrease diminished greatly. A plateau of oxygen uptake was established during this time by ninety per cent (9 of 10) of the dehydrated female rats and by eighty per cent (12 of 15) of the male dehydrates. Some animals were seen to break the progressive decrease in oxygen uptake by exceeding, during this time, the level recorded for the previous day, or days (Plate III).

This plateau of oxygen consumption was followed by a sudden large drop in oxygen uptake (Table I). The dehydrated male rats gave this response almost exclusively on day seven of dehydration. The female dehydrates gave this response more commonly on the sixth day of dehydration although this is not well shown by Table I.

The oxygen consumption values for the watered control male rats in experiments III, IV, and VI, when averaged together, ran very close to the average of the base level values established for these groups (Table I). The controls for experiments III, IV, and the watered control females for experiment V, when analyzed separately, ran far below their respective base level values on several of the test days. The control males in experiment VI averaged slightly above their base level values each day of testing.

The only consistent fluctuation observed in oxygen consumption among the control animals, especially in experiments III and IV, was the drop in oxygen uptake on control day six (Table I). There was a mild tendency for the controls to return to a high oxygen consumption value on control day seven. Neither of these fluctuations correspond with the leveling off and then sudden decrease in oxygen consumption observed in

Table 1. Average daily oxygen consumption values for the various test groups. *

| GROUP | DAY OF TESTING | | | | | | | |
|---|--------------------------------|---------|-------|-------|-------|---------|---------|---------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Expt. I, 5 females. | 89.3 | 78.4 | 72.2 | 61.7 | 68.2 | 61.1 | 51.8(2) | .. |
| Expt. II, 5 females. | 87.0(4) ^a | 74.3 | 65.0 | 70.2 | 62.9 | 63.6(4) | 59.0(3) | 54.6(4) |
| Expt. III, 5 male dehydrates. | 86.0 | 75.0 | 70.3 | 60.0 | 59.0 | 60.0 | 51.2 | .. |
| 5 male watered controls. | 95.0 | 95.0 | 96.0 | 93.0 | 98.0 | 92.5 | 104.0 | 92.5 |
| Expt. IV, 5 male dehydrates. | 84.4 | 72.4 | 65.6 | 64.4 | 58.6 | 58.4 | 46.0 | 49.0(4) |
| 5 male watered controls. | 93.6 | 103.2 | 100.8 | 94.2 | 102.6 | 90.2 | 94.2 | 96.2 |
| Expt. V, 5 male dehydrates. | 89.4 | 80.7 | 77.8 | 70.0 | 66.4 | 63.0 | 55.2 | 59.0 |
| 4 female watered controls. | 101.3 | 93.1 | 102.3 | 96.5 | 92.5 | 92.4 | 92.0 | 94.1 |
| Average of entire group = 95.5 | | | | | | | | |
| Expt. VI, 5 male dehydrates. ... | 87.4 | 77.1(4) | 75.6 | 71.8 | 61.1 | 56.3 | 56.2 | 44.5 |
| 5 male watered controls. | 101.5 | 103.6 | 103.1 | 103.9 | 105.4 | 102.4 | 106.2 | 107.3 |
| 10 female dehydrates. | 88.3(9) | 76.4 | 68.6 | 65.9 | 65.5 | 62.2(9) | 56.1(5) | 54.6(4) |
| Expts. I and II, 15 male dehydrates. | 86.7 | 76.0 | 71.2 | 64.8 | 61.3 | 60.4 | 50.8 | 54.5(9) |
| Expts. III, IV, and V, 14 male watered controls. | 96.8 | 101.1 | 100.2 | 98.7 | 102.3 | 94.5 | 101.3 | 99.1 |
| Expts. III, IV, and VI. | Average of entire group = 99.2 | | | | | | | |

* All values are expressed in per cent of the base level average established for that group.

.. No data taken.

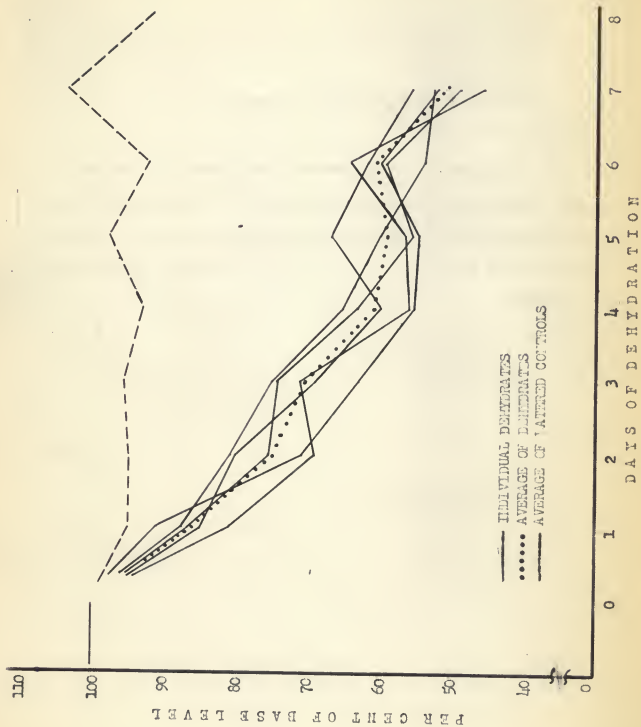
...Measurements not incorporated into this study.

^a Number in parenthesis denotes number of animals if less than that stated in the column at left.

EXPLANATION OF FIGURE III.

A graph showing oxygen consumption levels for the five male dehydrates and the five male watered controls from experiment III. Oxygen consumption values are expressed as per cent of the base level established for that animal, or of the group average.

PLATE III.



the dehydrated rats.

Daily oxygen consumption values for each rat used in this study are given in tabular form in the appendix. All values are given as per cent of the base level of oxygen consumption established for each animal.

Body Weights

Body weights of the dehydrated animals fell off rapidly after removal of the drinking water (Table 2). The weight loss for all dehydrates was relatively large during the first day of dehydration. Thereafter, the average day-to-day weight decrease proceeded at a lower and nearly constant rate. The average daily weight loss for the female dehydrates ranged from 8 to 13 grams. The range for the male dehydrates was 10 to 14 grams. After eight days of dehydration the females had an average loss of thirty-six per cent of their original body weight and the males an average loss of thirty-seven per cent of their original weight.

The watered control animals maintained or increased their weights slightly. The average weights for the male watered controls on days six and seven of dehydration were of interest. No attempt has been made to explain the possible relationship between these body weight changes and the oxygen consumption curves on test days six and seven for these same animals.

Table 2. Average body weights, in grams, of the various test groups.

| Days of Testing | 10 Female Dehydrates | 4 Female Watered Controls | 14 Male Watered Controls | 15 Male Dehydrates |
|-----------------|----------------------|---------------------------|--------------------------|--------------------|
| 0 | 262 | 286 | 292 | 308 |
| 1 | 238 | 284 | 292 | 281 |
| 2 | 225 | 284 | 295 | 269 |
| 3 | 213 | 284 | 300 | 255 |
| 4 | 203 | 285 | 303 | 242 |
| 5 | 192 | 285 | 308 | 231 |
| 6 | 184 | 288 | 307 | 219 |
| 7 | 175 | 288 | 313 | 208 |
| 8 | 167* | 285 | 313 | 198 |

* Average of five animals.

Food Consumption

No record of food consumption was kept for the control rats. An incomplete record was kept for certain of the dehydrated groups. The results shown in Table 3 agree with those of Reichlin (1957) in that feeding decreased rapidly and virtually ceased by day five of dehydration.

Table 3. Food consumption.

| Days Dehydration | 10 Male Dehydrates | | 5 Female Dehydrates | |
|------------------|--------------------|-------------|---------------------|-------------|
| | Food, in | | Food, in | |
| | : Per cent | | : Per cent | |
| | Grams. | : of Normal | Grams. | : of Normal |
| | | : Intake. | | : Intake. |
| 0 | 340 | 100.0 | 140 | 100 |
| 1 | 190 | 56.5 | 85 | 68 |
| 2 | 155 | 45.5 | 67 | 48 |
| 3 | 57 | 16.8 | 28 | 20 |
| 4 | 19 | 5.6 | 11 | 8 |
| 5 | 17 | 5.0 | 11 | 8 |
| 6 | -- | --- | -- | - |
| 7 | -- | --- | -- | - |
| 8 | -- | --- | -- | - |

DISCUSSION

Determination of the resting metabolic rate of an animal by the measurement of oxygen consumption is an accepted method of assessing the state of thyroid gland activity (West and Todd, 1959, p. 665). The thyroid gland is the primary regulator of the body metabolic rate; but various adrenocortical steroids are also known to enhance metabolism. However, it is difficult, especially during conditions of stress, to evaluate the role played by the adrenal cortex in the regulation of metabolism.

It has been shown, in the white rat and other animals, that while thyroid activity is often thought to be depressed, adrenal cortex activity is increased during adaptation to a wide variety of stress situations (Selye, 1946). The normally high levels of both cholesterol and ascorbic acid in the rat adrenal gland decrease markedly during stress or the injection of ACTH (Sayers and Sayers, 1957; Sayers and Sayers, 1946; Long, 1947). This has given rise to the view that the depletion of adrenal stores of cholesterol and ascorbic acid is an indication of accelerated adrenal cortex activity (Bessey, *et. al.*, 1953). It is thought that cholesterol serves as a precursor for cortical hormone synthesis and that ascorbic acid, in some unknown manner, is involved in the process (West and Todd, 1959, p. 401).

This hypothesis of ascorbic acid involvement in cortical secretion, and the implication that the ascorbic acid level is an index of adrenal cortex activity, has been questioned by some workers. Done, *et. al.* (1953) has shown that plasma concentrations of adrenal steroids in scorbutic guinea pigs may be tenfold that found in normal

controls. Stewart, et. al. (1952) observed that urinary excretion of 17-ketosteroids by scorbutic monkeys equaled or exceeded that of the controls. He concluded that adrenal function in scorbutic monkeys was normal. Oesterling (1951) has also observed apparently normal adrenal cortex function in the scorbutic guinea pig. Elton, et. al. (1959) tested the effects of ACTH injection and exposure to cold on the concentration of adrenal ascorbic acid and cholesterol in various animal species other than rats and guinea pigs. Exposure to severe cold significantly lowered adrenal ascorbic levels in opossums and dogs, but not in frogs, toads, chickens, mice, hamsters, rabbits, and cats. ACTH injections significantly decreased ascorbic acid levels only in opossums, mice, and hamsters. Exposure to cold increased adrenal cholesterol concentration only in rabbits; the other species were largely unchanged. ACTH injection increased the cholesterol level in frogs only. None of these studies included work with the white rat.

In the white rat a wide variety of stressor agents has been shown to lower the ascorbic acid concentration of the adrenal gland. However, rats deprived of food and water for from 48 to 72 hours by Kimura (1954) displayed adrenal ascorbic levels higher than those of the controls. Swartz (1960), working with rats deprived of water for eight days, observed an increase in adrenal ascorbic acid levels from the second through the sixth day of dehydration; after day six of dehydration the ascorbic acid levels dropped below that of the controls.

It is not understood why the rat should respond to the stress of dehydration, and the accompanying decrease in food intake, with an apparent increase in the adrenal ascorbic acid level. Further, it is not understood whether or not this should be interpreted as meaning

that adrenal cortex activity is not significantly increased in response to this stress situation. If cortex activity was not significantly increased during the present dehydration study the diminution in the rate of decrease of oxygen consumption observed from days four through six of dehydration could possibly be attributed to increased thyroid activity during this period. This agrees with the findings by Swartz of increased protein-bound iodine levels from the fourth through the sixth day of dehydration; the dehydrated animals also displayed a small but significant increase over the controls in the height of the follicular epithelium. The findings of Reichlin (1957) are in conflict with these data. He observed both a lower plasma precipitable-iodine level and a progressive decrease in the release of I^{131} from the thyroid gland in rats deprived of water for seven days.

Another factor to be considered when attempting to interpret oxygen consumption data is the effect of the experimental method on the gas exchange. No respiratory quotient determinations were made during this study. Dehydration, and the accompanying starvation, limits the amount of carbohydrate metabolized and increases the amount of fat utilized by the body. More oxygen is needed to break down the oxygen-poor fat. Both ketosis and a lowering of the respiratory quotient result (West and Todd, 1959, p. 922). Farris and Griffith (1948) gave a mean respiratory quotient of 0.894 (range of 0.754-1.072) for sixty-eight determinations on eleven non-fasted white rats ranging from 120-201 grams in weight. Krantz and Carr (1935) calculated a mean respiratory quotient of 0.725 for ninety-two rats which had been fasted for forty-eight hours; a mean of 0.708 was obtained for the non-protein nitrogen R. Q. Wesson (1930) gave an average R. Q. of 0.733 for the

38th through the 44th hours of fasting in rats.

It is possible that, under these conditions, an animal experiencing a steadily decreasing metabolic rate could still show a very slow decrease, or even a temporary increase, in the rate of oxygen consumption from day-to-day. For example, using the oxygen uptake rate of 185 mg/100 grams of body weight/hour (Krantz and Carr, op. cit.) it is seen that a normal rat weighing 250 grams would consume approximately 355 cc. of oxygen during the one hour test period. With an R. Q. value of 0.894 (Farris and Griffith, op. cit.) this animal would expire some 317 cc. of carbon dioxide. As dehydration progresses both the metabolic rate and the volume of gas exchange decrease to below normal levels. It is assumed that the carbon dioxide output for an animal after six days of dehydration had fallen to sixty per cent of the normal level. At this time, with no change in the R. Q., oxygen consumption should be approximately 213 cc. and carbon dioxide output some 190 cc. But with a carbon dioxide output of some 190 cc., and a R. Q. value near 0.71 as previously discussed, the animal must have consumed some 268 cc. of oxygen during the test period. This 55 cc. increase in oxygen consumption, which is a significant part of the oxygen uptake of even a normal animal, could then possibly occur with no increase in the metabolic rate.

The ketosis which accompanies dehydration and starvation may also distort metabolic events. The rat is considered to be strongly resistant to starvation ketosis (West and Todd, 1959, p. 922). Smith (1926) fed diets composed largely of fat, protein, carbohydrate, or a balanced mixture of these to four groups of normal rats. The excretion of acetone bodies by individuals among the various groups varied only

1-3 mg/day. Smith also concluded that fasting produces no appreciable ketosis in the rat, but the length of the fasting period was not recorded. Fasting ketosis, to whatever degree it may occur in the rat, does occur in conditions of alkalosis according to West and Todd (op. cit., p. 923). They admit to not understanding the reasons behind alkalosis ketosis. Alkalosis causes an apparent decrease of the R. Q. since carbon dioxide is retained within the body in an attempt to raise the body pH. This may occur even without any change in the oxidation processes of the body (Fulton, 1955, p. 1044). Thus, any degree of alkalosis experienced by the dehydrated animals used in this study would have served to increase the validity of the recorded manometer data.

Further, fluctuations in the R. Q. during progressive dehydration and underfeeding do not appear to explain the sudden decrease in oxygen consumption seen in a high percentage of the test animals after seven days of dehydration. During the late stages of fasting, increasing amounts of protein are oxidized as the fat stores become depleted. The R. Q. rises. The average decrease in oxygen consumption recorded on day seven of dehydration for the group of fifteen male dehydrates equals approximately ten per cent of their average base level value, or approximately 40-45 cc. (Table I). In order for a change of the R. Q. to account entirely for this apparently sharp drop in oxygen uptake a shift upward from about 0.71 (the figure used previously) to near 0.80 would need to occur within twenty-four hours. It seems highly unlikely that this would occur. Secondly, these animals were not considered to be in the late stages of fasting after seven days of dehydration. The white rat has been known to survive for fifteen days after removal of

the drinking water. Finally, the older and much fatter male dehydrates in Experiment V displayed an average decrease from base level in oxygen consumption nearly identical with that shown by the much leaner male dehydrates in Experiment III. This result seems unlikely if the depletion of fat stores, the increased utilization of protein for energy, and the accompanying change of the R. Q. are fully to explain the similar oxygen consumption curves observed in the two groups.

SUMMARY AND CONCLUSIONS

Oxygen consumption, by white rats subjected to dehydration, decreased rapidly during the first three days. From day four through day six of dehydration, oxygen uptake levels remained between sixty and sixty-five per cent of the normal levels. In the male dehydrates this plateau was followed on day seven of dehydration by an average decrease to fifty-one per cent of the normal oxygen uptake levels. The female dehydrates gave a slightly smaller average decrease in oxygen consumption; and a high per cent of them displayed this drop on day six of dehydration.

Body weights of the dehydrated animals decreased an average of twenty-five grams during the first day of dehydration. Thereafter, the female dehydrates had an average daily weight loss of eight to thirteen grams and had lost thirty-six per cent of their original body weight after eight days of dehydration. The male dehydrates had an average daily weight loss of ten to fourteen grams and had lost thirty-seven per cent of their original body weight after eight days of dehydration. The watered control animals maintained or increased their weights

slightly.

An incomplete record of food consumption kept for certain of the dehydrated groups showed that food intake decreased rapidly to below fifty per cent of the normal level after two days of dehydration. Feeding had virtually ceased by day five of dehydration.

As feeding decreases the body obtains an increasingly higher per cent of its food energy from fat stores. The respiratory quotient is lowered as more oxygen is required to break down the oxygen-poor fat. No R. Q. determinations were made during this study. It is thought that an animal could consume a significantly larger amount of oxygen during this time without experiencing an increase in the metabolic rate, and that this situation could account for the plateau of oxygen consumption previously discussed. During the late stages of starvation the R. Q. rises as a result of the increased use of protein for food energy. But it is thought unlikely that the sudden decrease in oxygen uptake which was seen to occur on day six or seven of dehydration could be explained by this increase of the R. Q.

The relative importance of the thyroid and the adrenal glands in the oxygen consumption curves recorded for these dehydrated rats is not fully understood.

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APPENDIX

The daily oxygen consumption levels are given for each animal in the six experiments discussed in this paper. All values are expressed as per cent of the base level of oxygen consumption established for that animal prior to the beginning of testing. The daily average is also given for each test group of five animals.

Experiment I.

Table 1. Five dehydrated female rats.

| Day of Dehydration | Number of Test Animal | | | | | Group Average |
|-----------------------|-----------------------|------|------|------|------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 95.5 | 89.0 | 99.5 | 77.5 | 85.0 | 89.3 |
| 2 | 85.5 | 93.0 | 80.5 | 58.0 | 75.0 | 78.4 |
| 3 | 73.5 | 78.0 | 79.5 | 56.0 | 74.0 | 72.2 |
| 4 | 67.0 | 66.5 | 75.5 | 43.0 | 56.5 | 61.7 |
| 5 | 72.0 | 78.5 | 72.5 | 63.0 | 55.0 | 68.2 |
| 6 | 64.5 | 67.5 | 68.5 | 50.0 | 55.0 | 61.1 |
| 7 | 58.5 | ** | ** | 45.0 | ** | 51.8(2) |

Experiment II.

Table 2. Five dehydrated female rats.

| Control Day | Number of Test Animal | | | | | Group Average |
|----------------|-----------------------|-------|------|-------|-------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 82.0 | 85.5 | 92.0 | 88.5 | 97.0* | 87.0(4) |
| 2 | 61.5 | 69.0 | 85.0 | 71.0 | 85.0 | 74.3 |
| 3 | 57.0 | 73.0 | 52.5 | 60.5 | 82.0 | 65.0 |
| 4 | 72.5 | 76.0 | 73.0 | 62.0 | 67.5 | 70.2 |
| 5 | 57.5 | 63.0 | 63.0 | 49.0 | 82.0 | 62.9 |
| 6 | 56.5 | 69.0 | 58.0 | 61.5* | 71.0 | 63.6(4) |
| 7 | 53.5 | 63.0* | 58.5 | 59.0* | 65.0 | 59.0(3) |
| 8 | 40.0 | 59.0 | 58.0 | 62.5* | 61.5 | 54.6(4) |

* Value not incorporated into this study.

** No data taken.

() The correct number of animals, if less than five, used to calculate the group average.

Experiment III.

Table 3. Five dehydrated male rats.

| Day of | : | Number of Test Animal | | | | | : | Group | | | | |
|-------------|---|-----------------------|---|------|---|------|---|-------|---|------|---|---------|
| Dehydration | : | 1 | : | 2 | : | 3 | : | 4 | : | 5 | : | Average |
| 1 | | 87.0 | | 85.0 | | 81.0 | | 87.0 | | 91.0 | | 86.0 |
| 2 | | 76.0 | | 80.0 | | 69.0 | | 80.0 | | 70.5 | | 75.0 |
| 3 | | 74.0 | | 69.0 | | 71.0 | | 74.0 | | 63.5 | | 70.3 |
| 4 | | 63.0 | | 60.0 | | 56.0 | | 65.0 | | 56.0 | | 60.0 |
| 5 | | 56.0 | | 67.0 | | 57.0 | | 60.0 | | 55.0 | | 59.0 |
| 6 | | 59.0 | | 62.0 | | 64.0 | | 54.0 | | 60.0 | | 60.0 |
| 7 | | 49.0 | | 56.0 | | 46.0 | | 53.0 | | 52.0 | | 51.2 |

Table 4. Five watered male controls.

| Control | : | Number of Test Animal | | | | | : | Group | | | | |
|---------|---|-----------------------|---|-------|---|-------|---|-------|---|---|---|-------------|
| Day | : | 1 | : | 2 | : | 3 | : | 4 | : | 5 | : | Average (4) |
| 1 | | 94.0 | | 95.0 | | 94.0 | | 97.0 | | * | | 95.0 |
| 2 | | 98.0 | | 97.0 | | 91.0 | | 95.0 | | * | | 95.0 |
| 3 | | 102.0 | | 90.0 | | 96.0 | | 95.0 | | * | | 96.0 |
| 4 | | 93.0 | | 94.0 | | 92.0 | | 92.0 | | * | | 93.0 |
| 5 | | 98.0 | | 100.0 | | 96.0 | | 98.0 | | * | | 98.0 |
| 6 | | 91.0 | | 102.0 | | 90.0 | | 87.0 | | * | | 92.5 |
| 7 | | 104.0 | | 104.0 | | 102.0 | | 106.0 | | * | | 104.0 |
| 8 | | 97.0 | | 91.0 | | 95.0 | | 87.0 | | * | | 92.5 |

* Value not incorporated into this study.

** No data taken.

() Correct number of animals, if less than five, used to calculate the group averages.

Experiment IV.

Table 5. Five dehydrated male rats.

| Day of Dehydration | Number of Test Animal | | | | | Group Average |
|-----------------------|-----------------------|------|------|------|------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 86.0 | 92.0 | 80.0 | 86.0 | 80.0 | 84.8 |
| 2 | 84.0 | 77.0 | 61.0 | 65.0 | 75.0 | 72.4 |
| 3 | 68.0 | 72.0 | 58.0 | 59.0 | 71.0 | 65.6 |
| 4 | 72.0 | 67.0 | 62.0 | 57.0 | 64.0 | 64.4 |
| 5 | 60.0 | 64.0 | 58.0 | 52.0 | 59.0 | 58.6 |
| 6 | 55.0 | 63.0 | 56.0 | 61.0 | 57.0 | 58.4 |
| 7 | 48.0 | 47.0 | 45.0 | 42.0 | 48.0 | 46.0 |
| 8 | 77.0* | 55.0 | 44.0 | 49.0 | 48.0 | 49.0(4) |

Table 6. Five watered male controls.

| Control Day | Number of Test Animal | | | | | Group Average |
|----------------|-----------------------|-------|-------|-------|-------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 88.0 | 96.0 | 99.0 | 88.0 | 97.0 | 93.6 |
| 2 | 103.0 | 101.0 | 109.0 | 103.0 | 100.0 | 103.2 |
| 3 | 94.0 | 110.0 | 101.0 | 100.0 | 99.0 | 100.8 |
| 4 | 94.0 | 99.0 | 99.0 | 96.0 | 103.0 | 98.2 |
| 5 | 103.0 | 107.0 | 106.0 | 98.0 | 99.0 | 102.6 |
| 6 | 90.0 | 89.0 | 90.0 | 88.0 | 94.0 | 90.2 |
| 7 | 97.0 | 89.0 | 94.0 | 90.0 | 101.0 | 94.2 |
| 8 | 100.0 | 104.0 | 97.0 | 88.0 | 92.0 | 96.2 |

* Value not incorporated into this study.

() Correct number of animals, if less than five, used to calculated the group average.

Experiment V.

Table 7. Five dehydrated male rats.

| Day of Dehydration | Number of Test Animal | | | | | Group Average |
|-----------------------|-----------------------|------|------|------|------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 93.0 | 87.0 | 90.5 | 89.0 | 88.0 | 89.4 |
| 2 | 84.5 | 78.5 | 80.5 | 87.0 | 73.0 | 80.7 |
| 3 | 81.0 | 70.5 | 80.0 | 73.5 | 84.0 | 77.8 |
| 4 | 70.0 | 67.0 | 68.0 | 76.5 | 68.5 | 70.0 |
| 5 | 63.0 | 62.5 | 64.5 | 75.0 | 67.0 | 66.4 |
| 6 | 61.0 | 60.0 | 57.5 | 71.5 | 65.0 | 63.0 |
| 7 | 54.0 | 55.0 | 53.0 | 63.0 | 51.0 | 55.2 |
| 8 | 57.0 | 53.0 | 55.0 | 64.5 | 65.5 | 59.0 |

Table 8. Five watered female controls.

| Control Day | Number of Test Animal | | | | | Group Average (4) |
|----------------|-----------------------|---|-------|-------|-------|----------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 103.0 | * | 100.0 | 103.0 | 99.0 | 101.3 |
| 2 | 93.5 | * | 90.0 | 100.0 | 89.0 | 93.1 |
| 3 | 100.0 | * | 108.0 | 101.0 | 100.0 | 102.3 |
| 4 | 101.0 | * | 100.5 | 96.5 | 88.0 | 96.5 |
| 5 | 96.0 | * | 87.0 | 100.5 | 86.5 | 92.5 |
| 6 | 97.0 | * | 95.0 | 95.0 | 82.5 | 92.4 |
| 7 | 87.0 | * | 106.0 | 90.5 | 84.5 | 92.0 |
| 8 | 101.0 | * | 84.5 | 102.0 | 89.0 | 94.1 |

* Value not incorporated into this study.

() Correct number of animals, if less than five, used to calculate the group averages.

Experiment VI.

Table 9. Five dehydrated male rats.*

| Day of Dehydration | Number of Test Animal | | | | | Group Average |
|-----------------------|-----------------------|------|------|------|------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 88.5 | 91.0 | 87.5 | 85.0 | 85.0 | 87.4 |
| 2 | 72.0 | 78.0 | 85.0 | 78.5 | 80.0 | 78.7 |
| 3 | 75.5 | 68.0 | 79.5 | 82.5 | 72.5 | 75.6 |
| 4 | 66.5 | 67.5 | 72.0 | 85.0 | 68.0 | 71.8 |
| 5 | 64.0 | 59.0 | 59.0 | 64.5 | 59.0 | 61.1 |
| 6 | 61.5 | 54.0 | 52.0 | 58.0 | 56.0 | 56.3 |
| 7 | 58.0 | 63.5 | 52.5 | 53.5 | 53.5 | 56.2 |
| 8 | 45.0 | 54.5 | 45.0 | 29.0 | 49.0 | 44.5 |

Table 10. Five watered male controls.

| Control Day | Number of Test Animal | | | | | Group Average |
|----------------|-----------------------|-------|-------|-------|-------|------------------|
| | 1 | 2 | 3 | 4 | 5 | |
| 1 | 102.0 | 103.0 | 93.5 | 109.0 | 100.0 | 101.5 |
| 2 | 105.5 | 112.5 | 93.0 | 102.0 | 105.0 | 103.6 |
| 3 | 98.5 | 106.0 | 92.0 | 110.0 | 109.0 | 103.1 |
| 4 | 104.0 | 108.0 | 95.5 | 108.0 | 104.0 | 103.9 |
| 5 | 107.0 | 107.0 | 97.0 | 112.0 | 104.0 | 105.4 |
| 6 | 91.5 | 111.0 | 94.5 | 104.0 | 101.0 | 102.4 |
| 7 | 104.0 | 118.5 | 100.0 | 99.0 | 109.5 | 106.2 |
| 8 | 99.5 | 119.0 | 102.0 | 110.0 | 106.0 | 107.3 |

* Values not incorporated into this study.

A COMPARISON OF OXYGEN CONSUMPTION IN NORMAL
AND EXPERIMENTALLY DEHYDRATED RATS

by

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The purpose of this study was to compare the oxygen consumption of normal white rats with that of white rats subjected to experimental dehydration during a period of eight days.

Rats of both sexes, weighing between 235-380 grams, were used. The test and control animals for each experiment were of the same sex for all but one experiment. The animals were housed and tested in groups of five, were fed Purina Lab Chow and tapwater ad libitum, were marked with dyes for individual recognition, and were weighed prior to each daily measurement of oxygen consumption. Oxygen consumption determinations were made for a period of one hour on consecutive days. After being accustomed to the apparatus, and being tested for three days to establish a base level of oxygen consumption, both the control group and the group permitted to go without water were tested for seven to nine, usually eight, days.

The oxygen measurement apparatus consisted of a constant temperature water bath; a series of five chemical dessicators (250 mm. inside diameter) used as reaction flasks; and a series of five manometers containing Brodie's fluid and used to measure the pressure decrease within the reaction flasks. Sodalime was used as the carbon dioxide gas absorbent. The water bath temperature was 19 ± 0.5 C., and the room temperature was 22 ± 2 C. The reaction flasks had no outside oxygen source.

Measurements of relative oxygen consumption were made by recording the number of millimeters which the manometer fluid rose as a result of gas absorption within the flask. When the column of fluid had risen forty or fifty millimeters the system was opened to allow the fluid level and system pressure to return quickly to normal. The system was

then immediately closed and the fluid level allowed to rise once more. A thermobarometer was used to correct for any pressure fluctuations due to atmospheric or temperature changes.

Six experiments were discussed in this study. Experiments I and II each consisted of five dehydrated female rats. Experiments III, IV, and VI consisted of five dehydrated males and five watered male controls. Experiment V consisted of five dehydrated males and five watered female controls.

Oxygen consumption decreased rapidly during the first three days of dehydration, remained between sixty and sixty-five per cent of the normal levels from days four through six of dehydration, and decreased on day seven of dehydration, in the males, to an average of fifty-one per cent of the normal level. The female dehydrates gave a slightly smaller decrease in oxygen consumption, and more commonly on day six of dehydration.

Body weights of the dehydrated animals decreased an average of twenty-five grams during the first day of dehydration. Thereafter, the male dehydrates had an average daily weight loss of ten to fourteen grams; the average female weight loss was slightly less. After eight days of dehydration the males had lost thirty-seven per cent, and the females thirty-six per cent, of their original body weight.

Food consumption decreased rapidly to below fifty per cent of the normal level after two days of dehydration, and had virtually ceased by day five of dehydration.