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ENVIRONMENTAL TEMPERATURE AND DEPRIVATION OF FOOD AND WATER ON THE SPONTANEOUS ACTIVITY OF RATS†

INTRODUCTION

Deprivation of food, water, or individual nutrients usually causes an increase in the spontaneous running activity of the rat[3, 9, 10, 17, 18, 22, 27, 28, 30] although some exceptions have been reported.[2, 17, 30] The measurement of running activity has been used for investigations into motivation, for instance, as a measure of the hunger and thirst drives.[9, 10, 27] Wald and Jackson[30] considered the hyperactivity of rats during nutritional deprivation an example of mammalian emigration to relieve the nutritional pressure on the home population.

On the other hand, muscular activity is one of several means by which body temperature can be maintained through an increase in heat production.[4, 5, 7, 14] If the increased activity during starvation primarily reflects some function in the maintenance of body temperature, then there should be a relation between the environmental temperature and the degree of activity in starvation.

METHODS

Male Sprague-Dawley rats (300-400 gm.) were fed a synthetic diet (4.2 cal./gm.). In this diet approximately 70 per cent of the calories were derived from sucrose, 20 per cent from crude casein and 10 per cent from corn oil. Adequate amounts of the known necessary vitamins and salts were added to the mixture.[29] Food and water were provided *ad libitum,* except when one or the other was specifically restricted. The rats used in the acclimatization study were eight to nine weeks old at the beginning of the 28-week experiment. All other rats were 10 to 12 weeks old at the start of the experiments.

No other animals were kept in the experimental room and it was entered only for daily care and recording. The lights were automatically turned on at 8 a.m. and off at 8 p.m. The temperature of this room could be controlled to ± 1° C. at levels from 5

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to 35° C. The relative humidity was kept at 50 per cent, except at 10° C. and below when it could not be maintained and rose to about 90 per cent.

The animals lived in individual activity cages unless otherwise specified; some control studies were made in ordinary individual cages (7 x 9 x 6 inches). The activity cage consisted of a revolving drum, 14 inches in diameter, and a small living cage separable from the drum by a sliding door.* This door was never closed during these experiments. A Veedor counter recorded each complete revolution of the drum. Twelve of these cages were arranged in three rows on a specially constructed rack. As noted by Reed[17] the animals required about 10 days to adjust to the activity cage and showed a consistent level of activity following this period.

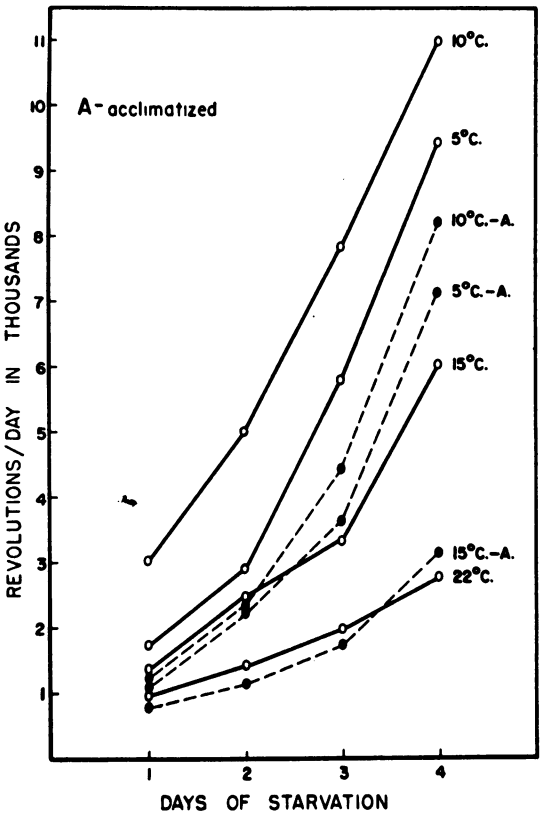

FIG. 1. The increases in spontaneous activity which occurred during four days of starvation at various environmental temperatures.

Skin and colonic temperatures were recorded by thermocouples.† The representative skin temperature was taken as the average of readings from three areas, the back, about one inch from the base of the tail, and the "thighs" of each hind leg. Each of these areas had been shaved. The colonic temperatures were obtained by inserting a rectal thermocouple 2 to 2½ inches past the anal orifice.

RESULTS

Figure 1 shows the increase in activity which occurred at environmental temperatures from 5° C. to 22° C. during four days of starvation. The running activity progressively increased up to the fourth day of food deprivation. The rate of increase was dependent on the surrounding temperature and was greatest in the cold environments. Curves at higher environmental temperatures (27°, 30°, 33° C.) are not shown since they were similar to,

* From Geo. H. Wahmann Mfg. Co., Baltimore, U.S.A.
† Electric thermometer manufactured by Light Laboratories, Brighton, England.

but shallower than, that at 22° C. Since the limit of survival for those animals in the cold was about four days, the fourth day was chosen for comparison of the activity at all environmental temperatures.

Figure 2 shows the spontaneous running activity of rats during the fed state and on the fourth day of starvation at environmental temperatures ranging from 5° to 33° C. In the fed state, the activity was about 1000 rev./day at environmental temperatures from 15° to 27° C., decreasing to 450 at 33° C. and to 700 at 5° C. This decrease in warm and cool environment has been noted by Reed.[17]

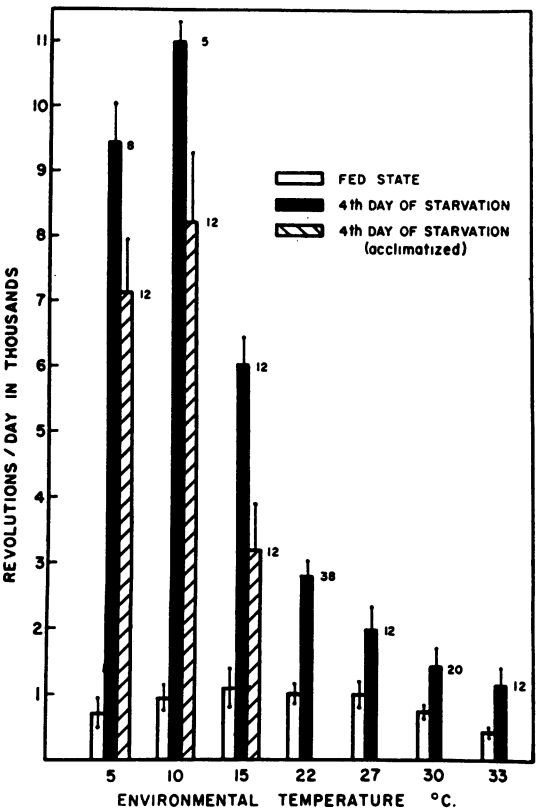

FIG. 2. The spontaneous running activity of rats in the fed state and on the fourth day of starvation at various environmental temperatures. Vertical lines represent the standard error.

During starvation there were increases in spontaneous activity which varied considerably with the environmental temperature. At 22° C. the average activity had risen to 2800 rev./day by the fourth day. In warmer environments the increase was less, reaching 1,150 at 33° C. At temperatures below 22° C. the activity showed very marked increases, rising to 6,000 at 15° C., 11,000 at 10° C., but only to 9,450 at 5° C. These animals at 15°, 10°, and 5° C. were groups of rats (originally 12 in each group) not fully acclimatized to the cold. They were adjusted to the activity cages at 22° C. and then exposed to one of the lower temperatures for 10 to 15 days before starvation.

Figure 2 also contains the results from 12 animals that were exposed to all the environmental temperatures studied. These animals were taken gradually from 33° to 5° C. over a period of seven months, with intervals

of adaptation, starvation, and recuperation at each of the designated temperatures. The time spent at each temperature was about four weeks. In view of the exposure to gradually decreasing temperatures and the time spent at each temperature, it is probable that these rats were fairly well acclimatized to the cold.[8, 23, 24, 25, 26] No acclimatization was evident in the activity of rats at temperatures of 22° C. and above.

The acclimatized rats displayed a lower average activity in starvation at 15°, 10°, and 5° C. than the corresponding nonacclimatized groups. None

TABLE 1. BODY WEIGHT LOSS DURING FOUR DAYS OF STARVATION

Env. temp. 0° C.	*Body weight loss (gm.)*		
	Activity cage		*Ordinary cage*
	Nonacclimatized	*Acclimatized*	
5	109	99	110
10	111	100	
15	72	64	
22	63		52
27	48		
30	48		
33	42		41

of the acclimatized animals died at any temperature during their four days of starvation, whereas in the nonacclimatized groups, seven died at 10° C. and four at 5° C. At 10° C. several of these animals were found prostrate and very cold on the fourth day of starvation after having run close to 13,000 revolutions during the previous 24 hours. Two of these animals were successfully revived by placing them in a warmer environment.

Table 1 shows the loss of body weight during the four days of starvation. Both the weight loss and the activity increased as the environmental temperature dropped. Rats of comparable weight were starved in ordinary individual cages at various environmental temperatures; these animals showed losses of body weight in four days similar to those of animals in the activity cages. At 22° C., the average length of survival in the ordinary cage was about nine days and in the activity cage about seven days. In the cold (5° C.) the survival was close to four days[19] after starvation in either type of cage.

Figure 3 demonstrates the effects of partial food restriction and complete water deprivation on the spontaneous activity and body weight loss when rats were given one-third (7 gm./day) of their voluntary food intake at 22° C. The daily activity gradually increased over a period of 17 days, when

maximal activity appeared to have been reached at slightly under 2,000 rev./day. This is lower than that observed in the completely starved rat. Refeeding resulted in an abrupt return to, or slightly below, the initial level of activity. This fall in activity on return of food was characteristic of ani-

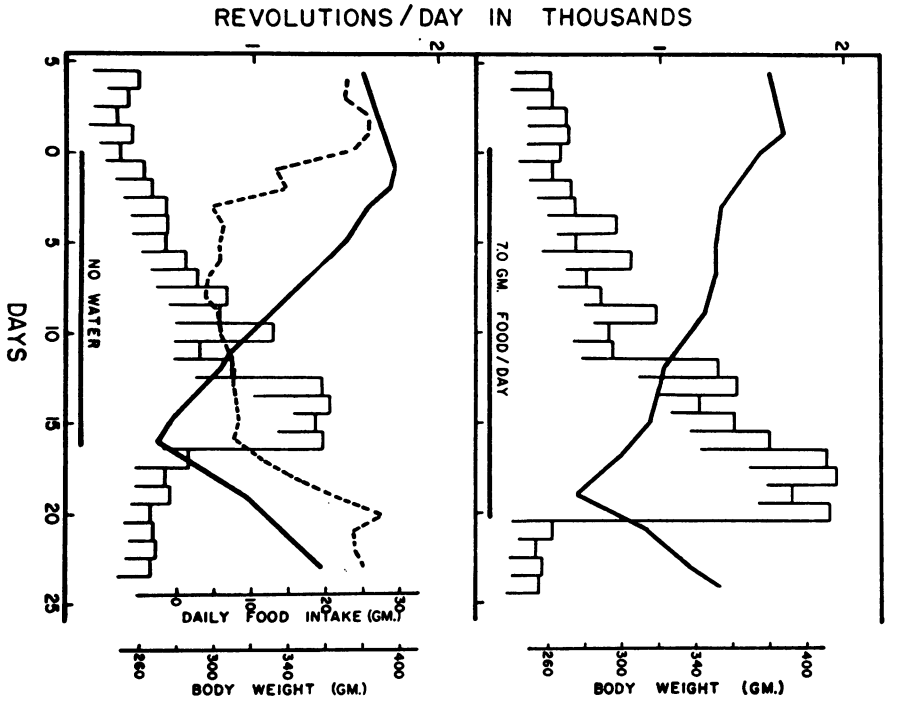

FIG. 3. The daily spontaneous activity, body weight loss, and food intake during (a) partial food and (b) complete water deprivation at an environmental temperature of 22° C. Eight rats were used in each study.

mals at all temperatures. Finger[9] also has reported a depression of activity following restoration of food.

Complete water restriction produced a similar picture. The activity increased gradually over a period of 13 days to form a plateau at close to 1,500 rev./day. The drop in activity on the first day after the return of water has also been observed by Finger and Reid,[10] but the depression below pre-thirst levels did not appear in our animals. For most of the period of water lack the food intake was about 7 gm./day but during maximal activity it was 8 gm./day.[cf.10] This food intake may account for the slightly lower maximal activity of these animals compared to the partial food-restricted group.

Preliminary experiments have been done on the skin and colonic temperatures of rats during starvation at 22° C. Figure 4 shows the temperature changes of rats in canvas slings, to minimize muscular activity, and in those allowed to move freely in ordinary individual cages (not activity cages). The animals starved in the slings showed a decline in both skin and colonic temperatures. The largest decrease was in the skin temperature. These

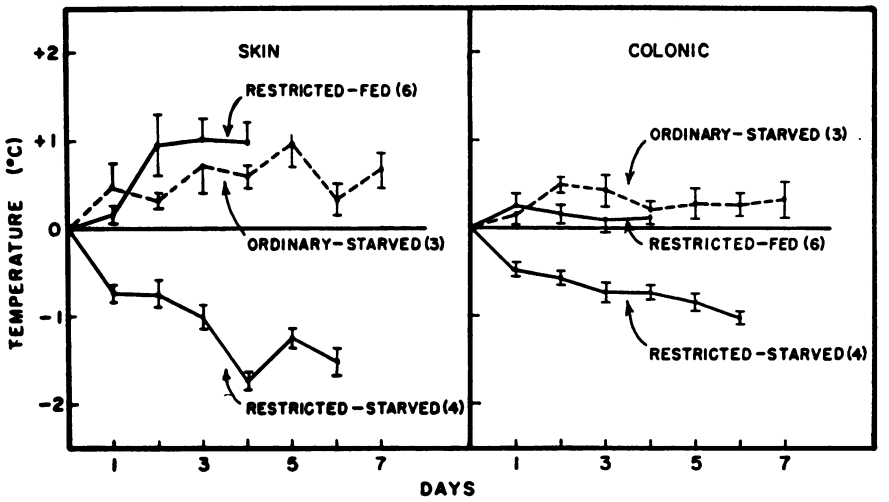

FIG. 4. The changes in skin and colonic temperatures of rats starved in canvas slings (Restricted-Starved), fed while in slings (Restricted-Fed) and starved but allowed to move freely in ordinary single cages (Ordinary-Starved). Vertical bars represent the standard error of the mean difference. Numbers in parenthesis represent number of animals. The environmental temperature was 22° C.

decreases did not appear in rats which were fed during a four-day period in the slings. Rats starved but allowed to move freely maintained their skin and colonic temperatures for at least the first six days of complete food deprivation.

DISCUSSION

Starvation causes an increase in the spontaneous activity of the rat. The inverse relation which we have observed between the level of the environmental temperature and the amount of activity supports the hypothesis that this increase in activity is related to the maintenance of body temperature in starvation. This hypothesis is further supported by our preliminary observations that the body temperature tends to fall in starvation when activity is restricted, but not when it is permitted.

A relation between activity and metabolic rate has long been considered[11,12,13,16,17,20] and it is well known that the metabolic rate increases as the environmental temperature falls.[1,8,19,23,24,28] Thus the great increase in activity upon starvation in the cold might be considered a reflection of the raised metabolic rate. The increase in metabolism on exposure to cold, however, occurs even in the fed state and in this state there is no increase in activity during exposure to cold. On the other hand, in a temperate environment, the metabolic rate usually falls as starvation progresses, but in the cold there is no fall in metabolic rate on starvation.[19] Thus, there seems to be little, if any, direct relation between the level of activity and the level of the basal metabolic rate in starvation.

If food is available *ad libitum,* rats maintain their colonic temperature, and may even increase it slightly, when exposed to a cold environment.[1,25] Starvation in man may cause temperature to fall to 35° C. and a diminished cutaneous circulation is suggested by pallor of the skin.[15] The present study indicates that, in the rat, starvation causes a fall in the core and peripheral temperature of the rat when activity is severely restricted, but not when activity is possible.

It appears from the similarity of the weight losses in the two cages that starvation increases the activity of rats in ordinary individual cages or in activity cages equally. Our methods of observation did not measure activity in the form of shivering and it is possible that the animals in the individual cages achieved a part of their increased muscular activity in this manner. Increased shivering may have decreased the running of acclimatized and nonacclimatized rats at 5° C. compared to that at 10° C.[8]

Bargeton *et al.*[1] have found that the heat production of acclimatized rats is less than that of nonacclimatized rats in a cold environment. From this it may be inferred that acclimatization is associated with a reduced loss of heat. And it is the acclimatized animals which show a smaller increase in activity on starvation in the cold. The improved conservation of heat has perhaps reduced the demand for its production to maintain body temperature.

The ability of the body to conserve heat is dependent on its effective insulation and this is increased in various ways in the acclimatized animal. Starvation undoubtedly causes a deterioration in this insulation; e.g. through catabolism of the subcutaneous fat. With the progress of starvation, the ability to conserve heat may thus steadily decline and lead to an increasing demand for the production of heat to maintain body temperature. This increasing demand could be supplied, in part at least, by a steady increase in muscular activity.

Brobeck[6] has supported the hypothesis that regulation of food intake is related to the regulation of body temperature. He and his colleagues[7] have also observed that a decline in body temperature precedes the rise in running activity that occurs with estrus and that the low activity in pseudopregnancy is associated with a high body temperature. Ryan[21] has recently shown that dinitrophenol causes a marked increase in the body temperature of dogs and it is known[11,19] that this drug, which increases the oxygen consumption and presumably the heat production, reduces activity.

Muscular activity appears to be closely related to the maintenance of body temperature, and to be interrelated with food intake in this function. The increase in activity on deprivation of water would not, at first, appear to support this conclusion, but even in this circumstance the degree of activity was related to the amount of food eaten.

SUMMARY

1. The running activity of rats increased in starvation. This increase in activity was inversely related to the environmental temperature between 33° and 10° C. and varied from 2 to 14 times that in the fed state. The activity at 5° C., however, was lower than that at 10° C.

2. Starvation did not produce as great an increase in the activity of acclimatized as in nonacclimatized rats at temperatures from 5° to 15° C.

3. The weight loss during four days of starvation in activity or in ordinary cages was similar and increased as the environmental temperature decreased.

4. Rats restricted to one-third (7.0 gm.) of their voluntary daily food intake, or completely deprived of water, increased their activity gradually and reached a maximum activity in 17 and 13 days, respectively. This activity was less than that after four days of starvation. The activity of the water deprived group was slightly less than that of the partial food-restricted animals but the food intake of the former was 8.0 gm. during maximal activity. Both groups showed a sudden drop to, or below, their initial level of activity on return of food or water *ad libitum*. This also occurred after complete starvation.

5. The rectal and skin temperatures decreased during starvation when activity was severely restricted, but not when the animals were fed and restricted simultaneously or starved with freedom of movement.

It is suggested that the increased activity during starvation is related to the maintenance of body temperature and is interrelated with food intake in this function.

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