RANDOM AND FOOD-DIRECTED ACTIVITY IN HYPERPHAGIC AND NORMAL RATS[1]

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Lesions in the vicinity of the ventromedial nuclei of the hypothalamus produce a striking behavioral change. After the operation, the animals eat two to three times as much as normal and gain weight very rapidly. This is the dynamic phase of hypothalamic hyperphagia, lasting from one to two months. After the animals become obese, the food intake decreases again to just slightly more than normal, and the high weight level remains fairly constant. This high plateau in weight level is the static phase of hypothalamic hyperphagia (2).

It is of some interest to determine whether this increase in food intake is accompanied by an increase in hunger drive as manifested by other behavioral measures which reflect the degree of food deprivation and satiation of the animal. These measures, such as activity level in a running wheel, bar-pressing performance to obtain food, speed of running down an alley to obtain food, etc., are measures of either random or food-directed activity. Both types of activity have been used as measures of the hunger drive (9, 12).

Therefore, the present experiment was performed to see whether the differences in eating behavior which exist between normal, dynamic hyperphagic, and obese hyperphagic animals are reflected in behavioral measures of random and food-directed activity.

METHOD

Experimental Groups

Three groups of female albino rats of the Wistar strain were used in each experiment: normal unoperated controls, obese hyperphagic animals, and recently operated nonobese hyperphagic animals. They were all approximately six months old. On the average, the normal group weighed 250 gm., the obese animals weighed 600 gm., and the nonobese hyperphagics weighed 270 gm.

In measuring random bodily activity, six animals were used in each group. In measuring food-directed activity, six normals, five obese, and five nonobese hyperphagics were used.

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Procedure

Hypothalamic lesions. Bilateral hypothalamic lesions were made with a stereotaxic instrument similar to that described by Stellar and Krause (10). After it was anesthetized and its skull exposed, the animal was placed in the stereotaxic instrument. Two holes were drilled in the skull with a dental trephine. Lesions were produced at points 1½ mm. posterior to the bregma, ¾ mm. lateral to the mid-line, and ½ mm. off the floor of the skull. A unipolar anode, 0.25 mm. in diameter and insulated except for 0.25 mm. at the tip, was used to pass a direct current of 1 ma. for 15 sec. The circuit was completed by means of a rectal cathode.

Measurement of random activity. Random bodily activity was measured in stabilimeter-type living cages, which were quite similar in construction to those described by Campbell (4). The basic unit consisted of a cylindrical wire-mesh cage balanced on a central pivot. Each cage was 9 in. in diameter and 12 in. high. The bottom and top were aluminum pans which snugly fitted the cylinder. The bottom pan was mounted on a central pivot. This pivot was a machine screw, 2½ in. long, which projected through the center of the bottom pan in such a manner that the cage tilted in different directions whenever the animal moved about the cage. Four microswitches were mounted underneath the cage floor, 90° apart around the perimeter of the pan. They allowed the cage to tip about ¼ in. in any direction, and were wired in such a manner that whenever the animal moved from one quadrant of the cage to another, a different pair of microswitches was depressed. This event was recorded automatically on an electromagnetic counter. A rod, ¼ in. in diameter, ran from the top to the bottom in the center of the cage. This prevented the animal from sitting in the center of the cage and teetering back and forth with slight shifts in weight.

Six of these cage units were mounted in two banks of three cages each. In each replication of the experiment, two animals in each group were assigned at random to the cages. Three replications of the experiment were run, and the cage assignments were such that the six different animals in each group were distributed equally in the six different cages.

Random activity was measured for three consecutive three-day periods—three days of ad libitum feeding, then three days of complete food deprivation, and finally three days of ad libitum feeding. The number of cage movements during each 24-hr. period was recorded. Each morning at 10 A.M., the counter readings were recorded, and each animal was removed from the cage and weighed. During the ad libitum feeding periods, Purina Laboratory Chow pellets were put in each cage. Unlimited water was available at all times throughout the experiment.

Measurement of food-directed activity. Food-directed activity was measured in a Skinner box. The box consisted of a cage, 8 in. high, 8½ in. wide, and 9 in. long. The two sides and the floor were made of ⅛-in. steel bars spaced ½ in. apart and mounted in two bakelite strips. The front and back were aluminum, and the top lid was clear Plexiglas to permit observation of the animal's behavior. Three inches above the floor, a lever projected ½ in. out into the cage through a slot in the front wall. The lever was 1⅞ in. wide, and could be depressed by a force of at least 10 gm. A small food cup, 1 in. square and ⅝ in. deep, projected from the front wall at a point 2½ in. below the bar and 1½ in. to the left of it.

Each time the animal pressed the bar and moved it through an arc of ⅛ in., a microswitch was closed and a feeder automatically delivered 90 mg. of food in the form of pellets. A water tube in the cage allowed free access to water at all times.

Each animal was trained to obtain pellets of food by pressing the bar and was allowed to eat ad libitum for a 12-hr. period each day. It was then removed from the box and placed in a living cage with water but no food for the next 12 hr. After a period of two to three days, each animal established a stable level of intake during each 12-hr. interval in the Skinner box. The effect on this intake of increasing the number of bar presses required for each food delivery was determined. Reinforcement ratios, i.e., the number of bar presses required for each food delivery, of 1, 4, 16, 64, and 256 were used in ascending order. Intake was measured for two consecutive 12-hr. periods on each ratio of reinforcement, and then the next higher ratio was used.

Results

Effect of Food Deprivation on Random Activity

In the analysis of random activity, heterogeneity of variance in activity between the three groups was found. A logarithmic transformation of the data was performed, and the significance of the differences is reported for the transformed scores. However, the differences were significant in both the transformed and untransformed scores.

Figure 1 presents the untransformed mean daily activity and shows the effect of food deprivation on random bodily activity. The normal animals show a much greater over-all level of random activity than do hyperphagic animals. Food deprivation produces a marked increase in the activity level of the normal animals, which is in turn followed by a sharp decrease in activity below the initial activity level, when the animals are allowed again to feed ad libitum. This effect is similar to the satiation syndrome reported by Finger (5).

The hyperphagic animals show much less effect of food deprivation on random activity.

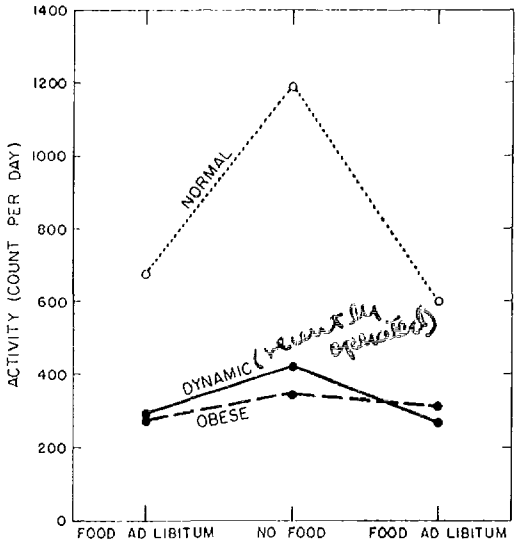

FIG. 1. Mean number of cage movements per day of normal, obese hyperphagic, and dynamic (nonobese) hyperphagic animals under conditions of ad libitum access to food and of complete food deprivation. Each point represents the activity of six animals measured for three days.

Dynamic hyperphagics show a small rise in activity, and a drop upon subsequent feeding ($F = 16.92$, $p < .01$). Both the rise and the fall in activity were significant at less than the .05 level. Obese hyperphagic animals show little or no effect of food deprivation on activity ($F = 2.99$, not significant).

Thus, in terms of the absolute magnitude of the effect of food deprivation, hyperphagics show less increase in random bodily activity than do normals.

If the effect of food deprivation is considered independent of the initial level of activity, the nonobese animals (both normal and dynamic hyperphagic) show a similar effect in that they show a rise in activity during food deprivation and then a sharp drop in activity during subsequent free feeding. The obese animals are relatively unaffected by the deprivation treatment. The fact that food deprivation has a different effect on the three groups was borne out by considering the activity during food deprivation and the combined average activity during both ad libitum food-intake periods. The difference in the effect of food deprivation on the three groups was shown by the interaction variance of groups by treatments. This was significant ($F = 3.68$, $p = .05$), and most

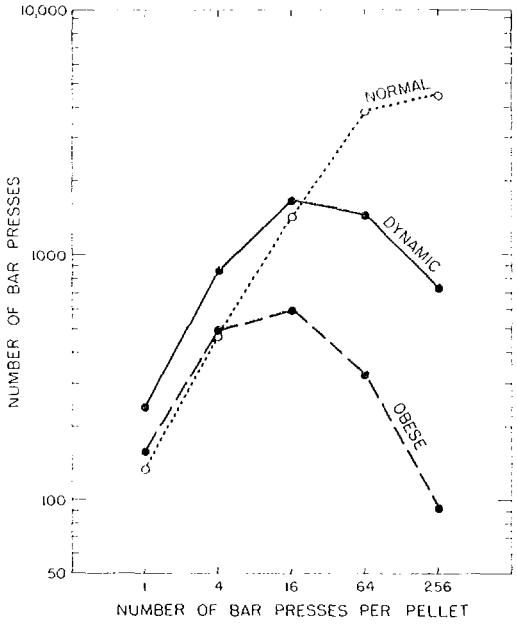

FIG. 2. Mean number of bar presses (per 12-hr. period) of normal, obese hyperphagic, and dynamic (nonobese) hyperphagic animals, as a function of the number of bar presses required to obtain each pellet.

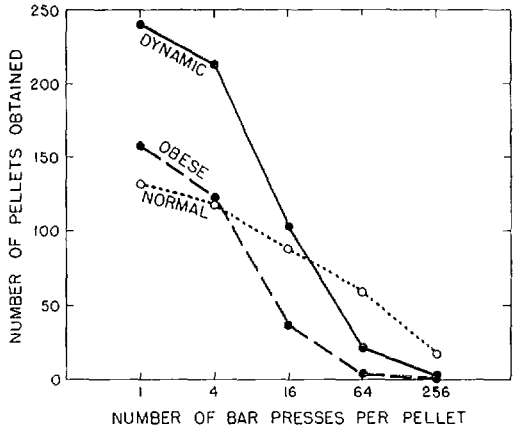

FIG. 3. Mean number of pellets obtained per 12-hr. period by normal, obese hyperphagic, and dynamic (nonobese) hyperphagic animals, as a function of the number of bar presses required to obtain each pellet.

of this interaction variance could be attributed to the difference in the effect of deprivation on obese versus nonobese animals.

Effect of Increased Work Requirement on Food-Directed Activity

The effect of an increased work requirement on bar-pressing activity is shown in Fig. 2 and 3. Figure 2 shows the effect of increasing the number of bar presses required to obtain each reinforcement, upon the number of bar presses during each 12-hr. period. Figure 3 shows the number of pellets obtained during each 12-hr. period as the number of bar presses required for each food delivery was increased. Similar phenomena are revealed in both figures, and so they will be discussed together.

When few bar presses are required to obtain each pellet, as with 1 and 4 bar presses per pellet, all animals press the bar and obtain quantities of food which essentially reflect their ad libitum food intake. When many bar presses are required to obtain each pellet, as with 64 and 256 bar presses per pellet, all animals fail to press the bar enough to obtain sufficient food to maintain a stable weight level.

At low ratios of reinforcement, such as 1 and 4, hyperphagic animals press the bar more and obtain more food than normal animals. At high ratios of reinforcement, such as 64 and 256, hyperphagic animals press the bar less and obtain less food than normal animals.

The effect of requiring an increase in the number of bar presses necessary to obtain each pellet is much more pronounced on the obese animals than on the dynamic hyperphagic animals. The obese animals sharply decrease the number of times that they press the bar at ratios of 64 and 256, and at a ratio of 256 will obtain no food for two days because they do not press the bar 256 times in the course of 12 hr. The dynamic hyperphagic animals decrease the number of times they press the bar more than do the normal animals, but they consistently work more than the obese animals.

DISCUSSION

These results indicate that the difference between the eating behavior of dynamic hyperphagic animals, which weigh essentially the same as normal animals, and that of obese hyperphagics is also reflected in measures of their random and food-directed activity. Food deprivation produces a greater effect on the random activity of dynamic hyperphagic animals than it does on the activity of obese hyperphagic animals. Dynamic hyperphagics also press the bar more than obese animals when there is an increase in the amount of work required to obtain each pellet of food.

When compared with normal animals, however, hyperphagic animals, both dynamic and obese, seem to respond less to food deprivation. This is indicated by the much smaller change in random bodily activity. It is also shown by the fact that an increase in the amount of work required to obtain each pellet of food will markedly decrease the work output of hyperphagic animals long before the normal animals are so affected.

The present results confirm and extend the previous findings of Miller, Bailey, and Stevenson (9), who reported that hyperphagic animals show a lower than normal level of performance in tasks requiring food-directed activity. In addition, the present experiment indicates that the effect of deprivation on nonobese animals is much more marked than on obese animals. This is in accordance with the fact that obese animals will completely reject diets adulterated with cellulose, kaolin, or quinine, whereas the intake of nonobese animals is much less affected (8, 11). It also agrees with the recent findings of Hollifield et al. (7), who showed that the activity of mice which became obese after gold thioglucose injection was not affected by food deprivation. It is possible that the level of the fat stores, which appears to be important in regulating the food intake of hyperphagic animals (8), is also important in determining the effect of food deprivation on performance measures of hunger drive.

In tasks where relatively little work is required to obtain each pellet of food, food-directed activity essentially reflects the ad libitum food intake of the animals. Thus, on ratios of 1 and 4 in the present experiment, the amount of food obtained by the animals paralleled closely the relative amounts of food they would obtain in a free-feeding situation.

In the bar-pressing situation, the effect on the food-intake level of requiring an increase in the number of bar presses necessary to obtain each pellet depends on many factors. The amount of training the animal has had, the time it is allowed to remain in the box each day, the height of the bar and its relation to the food cup, the amount of force necessary to depress the bar, and the maximum rate of pressing the bar which is limited by the excursion of the bar on each stroke will all determine the bar-pressing performance. It is therefore possible to obtain bar-pressing activity which reflects normal food intake at ratios higher than those which reflected normal food intake in the 12-hr. period used in the present experiment. Thus, in an experiment by Anliker and Mayer (1), 24-hr. food-intake cycles in normal and obese mice have been revealed in a bar-pressing situation using a ratio of 25 bar presses per pellet.

In evaluating hunger drive on the basis of measures of random and food-directed activity, the interpretation is complicated by the fact that hyperphagic animals display a much lower level of spontaneous bodily activity than do normal animals. This has been reported in measures of running-wheel activity (3, 6), and is clearly shown in the random bodily activity measured in the present experiment. There is at present no adequate explanation for the lowered level of spontaneous bodily activity which accompanies hypothalamic hyperphagia. It is apparently an additional effect of the hypothalamic lesions, but it does not seem to bear any clear relation to the exaggerated food intake. However, it is clear that there is a lowered level of bodily activity which is superimposed on both the random and food-directed activity of hypothalamic hyperphagic animals.

It is possible, therefore, that the decreased effect of food deprivation on the activity of hyperphagic rats as compared with normal animals might be interpreted as being due entirely to the initially low level of activity that the hyperphagic animals exhibit. However, in the bar-pressing situation, when few bar-presses are required for each pellet, hyperphagic animals press the bar more and obtain more food than do normal animals. When many bar-presses are required for each pellet, hyperphagic animals will often decrease their total work output to a point even less than the work performed when few bar-presses were required for each pellet. The decreased work output is especially noticeable in the obese animals. This seems to indicate, in support of Miller, Bailey, and Stevenson (9), that hyperphagic animals do indeed show a decrease in the drive to obtain food.

SUMMARY

Random and food-directed activity were used as measures of hunger drive in three groups of rats: normal unoperated controls, obese hypothalamic hyperphagic animals, and

recently operated nonobese hyperphagic animals.

Random bodily activity was measured in stabilimeter-type living cages, for three, three-day periods—before, during, and after complete food deprivation.

Food-directed activity was measured in a Skinner box. The animals were trained to obtain pellets of food by pressing the bar and were allowed to establish a stable 12-hr. food-intake level. The effect on this intake of increasing the number of bar presses required for each pellet was determined.

Normal animals showed greater random bodily activity than hyperphagic animals. The increase in activity during food-deprivation was greater in normal than in hyperphagic animals.

Food deprivation produced a greater effect on nonobese hyperphagic animals than on obese hyperphagics. The random activity of dynamic hyperphagic animals increased during food deprivation, but obese animals showed no significant change.

In the bar-pressing situation, when few bar presses were required for each pellet, hyperphagics pressed the bar more and obtained more food than normals. When many bar presses were required for each pellet, hyperphagics pressed the bar less and obtained less food than normals. This effect of increased work was more pronounced in obese than in nonobese hyperphagic animals.

It was concluded that:

1. On the basis of measures of random and food-directed activity, hyperphagic animals, especially obese animals, show a lower-than-normal drive to obtain food.

2. Food deprivation produces a greater effect on nonobese than on obese animals.

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