# EFFECTS OF SUBCORTICAL BRAIN DAMAGE ON HOARDING BEHAVIOUR

# THE EFFECTS OF SUBCORTICAL BRAIN DAMAGE
# ON
# HOARDING, NEST BUILDING, AND AVOIDANCE BEHAVIOUR
# IN THE RAT

By

JO-ANN LINDA BENTLEY, B.A.

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AUTHOR: Jo-Ann Linda Bentley, B.A. (McMaster University)

SUPERVISOR: C.H. Vanderwolf

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SCOPE AND CONTENTS:

A review of anatomical and behavioural studies of the limbic system suggests that some structures which Papez proposed as the central mechanism of emotion might be involved in food hoarding behaviour. Various structures in Papez' circuit were destroyed surgically and observations were taken on subsequent changes in food hoarding behaviour. In addition, observations were made on nest building behaviour and on avoidance performance. It was found that rats with bilateral damgge to the mammillothalamic tract and mammillary body were severely depressed in hoarding and avoidance behaviour. Septal damage caused a less severe deficit in both behaviours while hippocampal, fornical or thalamic damage did not have a significant effect.

A pilot study of hoarding behaviour in the hamster was carried out.

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# INTRODUCTION

Many different animals in their natural environment carry various materials to their home area. The experimental investigation of this "hoarding" behaviour did not begin however, until the work of Wolfe (1939). In the typical hoarding experiment, a rat is kept in an individual cage which has a sliding door leading to an alley or runway, which has at its far end a bin containing the material to be hoarded, usually pellets of rat food. The sliding door is opened daily for a short period, usually about one-half hour, and the number of pellets which the rat collects during this time is a measure of its hoarding activity. The onset of hoarding is generally abrupt and the activity then continues for the duration of the experiment.

Many variables have been found to influence hoarding. Among these are diet and metabolism, age, environment, and neural factors.

## Diet and Metabolism

It seems clear that diet has considerable effect on hoarding. For instance, it is generally agreed that food deprivation enhances hoarding. Although Porter (1951) found that deprivation is not a necessary condition for eliciting hoarding activity, all investigators report that it facilitates the onset of hoarding in rats and increases the amount hoarded.

Considerable work has been done on the effect of nutritional deficiences. Wolfe in his original 1939 experiment investigated the role of adequacy of diet by supplementing rat pellets with milk, lettuce, and cod liver oil. He found that the enriched group hoarded only .9 pellets per rat as compared with a control group fed enough regular lab pellets to maintain body weight, who hoarded 47.6 pellets per rat. The results of this study would have been more clear-cut if he had used a group of controls which were fed pellets ad libitum rather than a quantity just sufficient to maintain body weight, since the latter quantity of pellets for young rats constitutes deprivation.

Bindra (1948a) investigated the nutritional deficit hypothesis by feeding rats diets lacking in either carbohydrates, or proteins, or minerals, while a control group was fed a normal diet. He did not find any difference attributable to the depletion in the body of any specific components of normal diet. These results at first glance may seem to contradict those of Wolfe.

However, Bindra avoided the deprivation problem by allowing his animals free access to food. Moreover, Wolfe was adding supplements to the normal lab pellet diet, while Bindra was depriving the animals of elements of this diet.

Vitamin deficiency, however, seems to be important. Gross and Cohn (1954) studied the effect on hoarding behaviour of feeding rats a diet lacking in vitamin-B. After 38 to 46 days of deprivation, they hoarded significantly more normal pellets (as compared with vitamin-B deficient pellets) than they had during the initial control tests before vitamin-B deficiency diet. After the animals had been returned to the normal diet for periods of 46 to 53 days, all 12 animals hoarded signifigantly fewer normal pellets than they had at the end of the vitamin-B deprivation. Further effects of nutrition on hoarding were shown by a study of Gross, Fisher, and Cohn (1955) in which young rats were tested in a hoarding situation before and after being fed a rachitogenic diet for various lengths of time. Short periods of deprivation (20 days) produced no preference for normal pellets; however, longer periods of time (40 days) produced a preference for normal pellets in a situation permitting a choice between normal and vitamin-D deficient pellets in 17 out of 18 animals. The preference was retained when the position of the normal pellets was changed, and when the two types of pellets were mixed in a common bin. Feeding the animals a normal diet after the deprivation period, resulted in a reduction of the percentage of normal pellets hoarded as compared with those hoarded during the period of vitamin-D deficiency. Thus it has been clearly shown that the type of food rats hoard is determined, in part at least, by the diet on which the animals are maintained.

Stellar (1951) tested the hypothesis that a general metabolic change was the basis of hoarding. He depressed thyroid activity by administering thiouracil to one group, while another group was thyroidectomized and still another was injected with thyroxin to elevate the metabolic rate. These treatments had no signifigant effect when animals were given 30 minute hoarding tests under conditions of deprivation and satiation, or when given 24 hour tests of hoarding. Previously, Stellar (1943) had tried to alter the carbohydrate balance by injecting epinephrine, insulin, or glucose shortly before the hoarding test. He hypothesized that epinephrine and glucose would depress hoarding since they tend to restore the blood sugar level of the deprived rat to a level similar to that of the satiated animal. He predicted insulin would increase hoarding sincd it lowers the blood sugar level in a way similar to food deprivation. Positive results were obtained only with epinephrine, which depressed hoarding. Epinephrine however, has been shown to depress other behaviour. For example, Kosman and Gerard (1955) found that epinephrine severely impaired the performance of a conditioned avoidance response. They concluded that this was probably due to a general effect of the drug on activity and motor capabilities. Therefore, Stellar's experiment does not clearly demonstrate that any metabolic change is the basis for hoarding.

### Age

Very little research has been done on the variable of age. In a number of studies, the age of the subjects has not been reported and in most others, age differences have been disregarded. The only definitive study which has been published is that by Porter, Webster, and Licklider (1951) who tested seven groups of rats, the youngest shortly after weaning, and the oldest at 328 days. Their results showed that the number of pellets hoarded was directly proportional to the logarithm of the animal's age.

There are several possible interpretations of these findings. First, the superiority in hoarding of the oldest rats might be attributed to their greater experience in manipulating pellets (Marx, 1950; Porter, Webster, and Licklider, 1951; Wolfe, 1939). Alternatively, the older rats might have experienced more competition for food, more stress in feedings, and consequently have been repeatedly deprived. It is also conceivable that the late development of hoarding is not dependent on special learning experiences at all, but that the essential instinctual mechanism simply matures slowly. This explanation however is doubtful as some investigators (Hunt, 1941; Hunt, Schlosberg, Solomon, Stellar, 1947) have found that early feeding frustration experience did increase adult hoarding.

## Environmental Variables

The observation by McCleary and Morgan (1946) that animals in a natural habitat begin hoarding when the temperature falls lead them to explore this relation in the laboratory. By keeping animals in the winter in an unheated attic (temperature range 8° to 34° C), they found that the logarithm of the hoarding scores was inversely related to the environmental temperature.

Miller and Postman (1946) studied the effect of social conditions on hoarding. They allowed rats which had been reared together with a central food bin to hoard simultaneously from the same bin and found some rats showed a preference for hoarding from the central bin, while others hoarded more from the cages of the other rats. The occurrence of inter-cage hoarding and the lack of resistance by the rats whose hoards were stolen were interpreted as evidence supporting the hypothesis that the goal is the hoarding activity itself rather than the result of such activity. Denenberg (1952) using group-reared rats, found that rats hoarded more pellets under isolated conditions than in group conditions. Also, Ross, Smith, and Denenberg (1950) using rats reared alone, found hoarding scores decreased when other rats were introduced. Denenberg suggested that the social facilitation of eating under group conditions, interferes with the hoarding behaviour.

Hoarding is also affected by the specific conditions surrounding the home area. For example, Marx, Iawahara, and Brownstein (1957) and Waddell (1951) found that illuminating the alley greatly facilitated hoarding. Bindra (1948b) found that open plank alleys also increased hoarding. Miller and Viek (1944) found that the familiar odor and appearance of the home cage were important factors since changes resulted in a significant decrease in hoarding. Thus, since hoarding seems to depend on many sensory factors, interferences with neural structures should result in changed hoarding levels.

### Neural Basis of Hoarding Behaviour

The studies that have been reviewed suggest some of the conditions necessary for hoarding. The few studies that have attempted to probe the physiology of hoarding, have been directed toward the investigation of biochemical and metabolic factors. Little is known about the neurophysiology of hoarding.

Zubek (1951) was the first investigator to explore the involvement of the cortex in hoarding. He found that small neocortical lesions, regardless of location, <u>increased</u> the level of hoarding. He found this result surprising; he felt that since cortical lesions in the rat were certain to involve the removal of one or more sensory areas, one would expect that operations would make the hoarding situation appear less familiar to the animal, and (as Bindra 1948b found with normal animals), decreased familiarity might decrease hoarding. This was not the case. One possible hypothesis suggested by Zubek was that hoarding is a relatively primitive response integrated at the subcortical level and that the increase in hoarding was due to the release of some subcortical structures from the inhibitory influence of the cortex. After reviewing the studies of Beach (1943, 1944) which showed that maternal behaviour and copulation were greatly impaired by cortical lesions and that the degree of impairment was roughly correlated with the size of the lesion, Zubek suggested that hoarding may be a more primitive response than maternal behaviour or copulation and therefore becomes more prominent in the absence of the cortex.

It seems that the median cortical strip is particularly important in hoarding. Stamm (1953) studied the effect of cortical lesions which were larger than those produced by Zubek. He removed from 23 to 40 percent of the cortex and found that small lesions excluding the median cortical strip again increased hoarding whereas large lesions including this area, resulted in hoarding deficits. He also reported that after the operation each rat continued his individual pre-operative hoarding pattern.

In a later experiment (1954) Stamm divided rats into a group receiving damage along the dorsolateral surface of the cortex, and another group receiving similar damage along the median cortex. He found that the dorsolateral lesions did not effect hoarding, a result which is somewhat surprising in view of his earlier study and of Zubek's work. The lesions in the later experiment were however, somewhat larger. The median cortical lesions however, caused a marked decrease in the number of pellets hoarded but no difference in the other measure of hoarding performamce, the latency of alley entrance. Stamm concluded by suggesting that the median cortical strip performs some function similar to those ascribed to the frontal lobes in higher mammals.

In the previous two experiments, Stamm tested his animals both before and after surgery. In 1955 he subjected naive rats to bilateral lesions of the median cortex. Extensive damage (29 to 59 percent) caused a reduction in hoarding behaviour, but did not eliminate it.

Even after a latent period of several weeks, hoarding proceeded smoothly and rapidly.

These findings of Stamm have recently been confirmed by Bunnell, Friel, and Flesher (1966) who found that lesions of the median cortex in hamsters also produced severe disruptions in hoarding.

From these studies it can be concluded that the median cortical strip is involved in the performance of hoarding in rats and hamsters. Since the cingulate gyrus is part of the median cortical strip, it seems likely that the limbic system is involved.

## Limbic System and Hoarding

Papez in 1937 proposed that the hypothalmus, the anterior thalamic nuclei, the cingulate gyrus, the hippocampus and their interconnections constitute a unified mechanism which may "elaborate the functions of central emotion", as well as participate in emotional expression. Impulses of cortical origin would pass first to the hippocampal formation via the temporo-ammonic tracts, and then down by way of the fornix and mammillary body. From this they would pass upward through the mammillothalamic tract to the anterior nucleus of the thalamus and then by the medial thalamocortical radiation (in the cingulum) to the cortex of the cingulate gyrus. Papez cites clinical evidence suggesting that there is a loss of emotional dynamics as a result of disturbances to the mammillary body, anterior thalamus, or mammillothalamic tract.

Since 1937, developments in research and theory have lead to the idea that the limbic system plays a very general role in behaviour. Kluver and Bucy (1939) in a classic study, removed the temporal lobes in monkeys and found a peculiar syndrome that involved psychic blindness, oral tendencies, hypersexuality and hypermetamorphosis, or a "tendency to attend and react to every visual stimulus".

More recently, Pribram (1961) states that the essential function of the limbic system is the integration of behaviour components into smoothly functioning sequences. The changes in instinctive, affective, or other classes of behaviour which follow limbic manipulation are believed to be the result of alterations or disruptions of the sequencing of acts which comprise such complex behaviour.

Brady (1962) draws attention to the fact that at least some primitive pseudoaffective behavioural expression of emotion can be readily elicited at the mid-brain level even in the absence of all other forebrain structures. For example, sham rage behaviour can be found after removal of all cerebral tissue rostral, dorsal, and lateral to the hypothalamus.

MacLean (1964) has reviewed and elaborated Papez's earlier theoretical views on emotional behaviour and limbic system mechanisms, suggesting the basic importance of these forebrain structures not only for affective processes, but also for correlating "oral and visceral sensations" as well as "impressions from the sex organs, body wall, eye and ear".

Empirical support for MacLean's extensions of Papez's ideas comes from several recent studies. Fisher and Coury (1962) using cholinergic stimulation (carbachol) found that most of the brain areas that were positive for the drinking response were either part of the original Papez circuit or closely integrated with it. MacLean and Ploog's recent paper (1962) was concerned with identifying areas of primate brain in which electrical stimulation produced penile erection. Again there was a close correspondence of these areas with Papez's circuit. The circuit was also found by Robinson and Mishkin (1962) to be related to food and water ingestion after electrical stimulation. Further, Vanderwolf (1966, unpublished) suggested that the anterior thalamus and its connections to the cingulate cortex form part of a circuit concerned with hoarding. Since many of the areas implicated in these four separate studies are the same, the evidence appears strong that circuits mediating each of the primary drives will be found to follow generally parallel courses through the limbic system and diencephalon. Thus, from the anatomical predictions of Papez and the subsequent supporting behavioural evidence, it seemed to me that brain damage to this circuit in the rat and hamster would disrupt hoarding and perhaps related behaviour such as nest building. An avoidance experiment was included as a check on whether the operated rats were generally deteriorated or whether the brain damage had a specific effect on hoarding.

# METHOD

## Apparatus and Procedure

The purpose of these experiments was to test the effects of brain damage on hoarding behaviour, nest building, and a simple learning task.

The subjects were 58 male hooded rats, each weighing approximately 280 gm. and 14 male golden Syrian hamsters each weighing approximately 120 gm.

Two experiments on hoarding were carried out. The first experiment tested inexperienced rats and hamsters in the hoarding situation after surgery or sham surgery. In the second experiment rats were allowed to hoard food both before and after surgery. Comparison of the two types of experiments permits study of the effects of prior experience on the hoarding behaviour of brain damaged animals. After the hoarding tests were completed, all the rats were provided with nest material and observations were made on nest building behaviour. Finally, all rats were trained on an avoidance task.

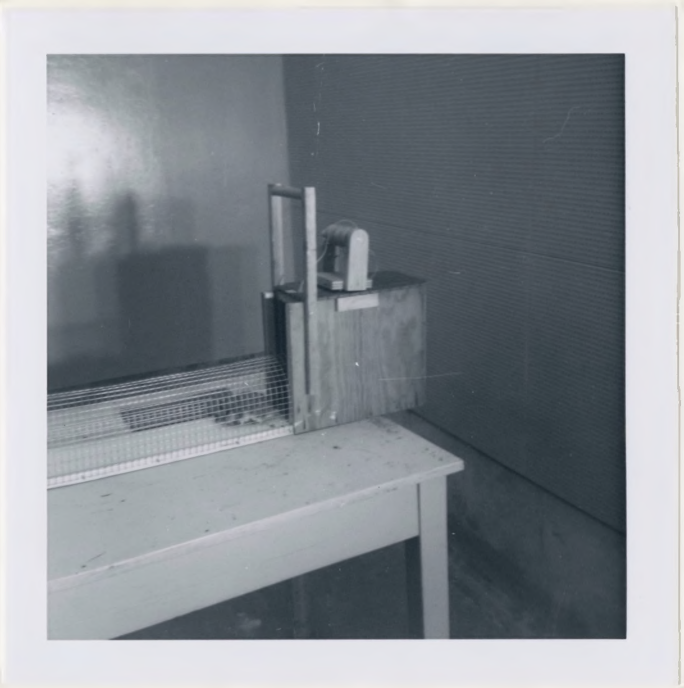
## Hoarding Test

The experiments on hoarding behaviour and nest building were conducted in a room maintained at a constant temperature (69°F) and humidity. Twelve hour periods of light and dark were alternated automatically, the light phase beginning approximately one and a half hours before testing commenced each morning.

The home cage (12 X 6½ X 11 in.) was constructed of wood painted black inside, with absorb-dri covering the floor. (See Figure 1.) The white wooden alley, (48 X 5 3/4 X 5 in.) was covered overhead by hardware cloth and was separated from the home cage by a guillotine door. There were 16 cages and in each replication of each experiment both brain damaged and control animals were tested simultaneously.

The procedure for inducing hoarding was as follows: each rat was placed in his home cage with the alley door closed, and given food and water ad libitum. After one week, a food deprivation schedule was begun so that in one week each rat's weight was reduced to 90 percent of what it had been at the start of the experiment. Next, tests of hoarding were started and were continued for 11 days. No food was available in the home cage during testing. Each day, 50 gm. of Purina Laboratory pellets were placed at the end of the alley and the home cage door was lifted, giving the rat access to the alley. Each test period was 25 minutes.

(a)



(b)

Fig. 1 (a) Home cage and hoarding alley with 50 gm. at alley end.
(b) Nest building apparatus in position on home cage.

During the first two days, all rats were tested in the same session, in the same room (to-gether condition). Although there was no physical contact, the rats could see, smell, and hear one another. After a test period each rat was weighed, the guillotine door was lowered, and the rat was returned to its home cage. The pellets remaining in the end of the alley were weighed, as were the pellets deposited in the home cage. Thus the amount of food eaten during the test could be calculated. Animals were always fed immediately after testing.

During the third to ninth days the animals were each tested separately for 25 minutes (the alone condition). A cage with its alley was lifted onto a table. The experimenter sat between two rooms so that two rats could be observed at the same time, yet each rat was alone in its room. The rats were able to see the experimenter. The guillotine doors were opened and the time spent by each animal in its alley (the rat was regarded as being in the alley only when all four feet were visible in the alley) was manually recorded on two channels of a Gerbrands recorder. This record also gave the latencies and total number of alley entrances during the test period. After testing, the rats were weighed and fed, and the total amount hoarded (in grams) was calculated as before. The tape from the recorder was analyzed by measuring the length of the pen deflections in millimeters and then converting this into seconds.

The tenth and eleventh hoarding test days were a replication of days one and two (together condition). Activity scores (that is the length of time spent in the alley, and the number of runs made) were not taken during the together condition.

For the rats that were tested after surgery only, an additional hoarding day followed day eleven. On this day 150 gm. of pellets, instead of the previous 50 were available. The test period was the usual 25 minutes.

### Experiment I : Hoarding test after surgery only

Experiment I consisted of 28 brain damaged animals which were tested after surgery only, and 23 naive control animals. These 23 naive animals were later subjected to surgery in experiment II. An additional control group consisted of 6 sham operated rats who received drill holes only, leaving the dura unbroken and one animal who received a bilateral subcortical mechanical puncture.

### Experiment II : Hoarding test before and after surgery

All rats in experiment II were given the complete 11 day hoarding test both before and after surgery. The procedure was identical to that of experiment I except that the amount of food eaten during the daily hoarding test was not recorded. Surgery was performed during the week following the first test and the identical test repeated two weeks later. Twelve animals received brain damage and 10 control animals received a sham operation. The sham operations were of three types: two control rats received bilateral drill holes leaving the dura unbroken; two rats received a bilateral cortical mechanical puncture; and six rats received a bilateral subcortical mechanical puncture.

### Hamster Hoarding Test

The procedure used for the hamster hoarding experiment differed slightly from that described above. A pilot study revealed that hamsters hoarded food much more reliably than rats and did so even when abundant food was available. Therefore, the hamsters were never food deprived and were tested for five days only. Four animals were tested for an additional period of seven days in order to take records of activity during hoarding.

### Nest Building

After the final day of hoarding tests, all rats were tested for their ability to build a nest. A ball of jute twine was suspended from the roof of each home cage and the rat was given 24 hours to pull down the string and build a nest. The nests were rated according to size.

## Avoidance Test

At the conclusion of the nest building experiment, all animals (except the hamsters) were trained on an avoidance task.

The avoidance apparatus was a large box divided into two compartments each measuring 10 x 18 x 18 in. One compartment was painted black, the other white, and each had a grid floor. These compartments were separated by a sliding door. A shock of about 1.0 ma could be delivered to the grid of the black compartment by a manually operated button.

The rat was allowed to wander freely in the box for 5 min. before testing commenced. Then, the rat was placed facing away from the door. If it failed to make the avoidance response of running to the white compartment within 5 sec. the shock was applied until an escape response occurred, or for a 30 sec. maximum. If the rat did not escape, it was put in the white compartment for the following 30 sec. A sliding door prevented re-entry into the black compartment. Trials were continued until the criterion of eight consecutive avoidances were made, or for a maximum of 30 trials. The latency of each avoidance response was recorded, as well as the total number of shocks received.

## Surgical and histological procedures

All surgery was performed under Nembutal anesthesia (plus chloral hydrate supplement for hamsters). Atropine and penicillin were always administered.

Rats were placed in a Stoelting or Scientific Prototype stereotaxic instrument and electrolytic lesions were made in the anterior thalamus, septum, hippocampus, and mammillothalamic tract. Brain structures were localized with the aid of the stereotaxic atlases of Kreig (1947) or de Groot (1959). Hamsters were held by the Scientific Prototype stereotaxic and the atlas and procedure of Smith and Bodemer (1963) was used.

The intracranial electrode was made of two strands of twisted insulated Nichrome wire (0.01 in. in diameter) with the insulation removed from the tips. A needle placed under the tail skin was the negative electrode. Bilateral lesions were created by 2.5 ma anodal current which flowed for 20 sec. on each side.

In five hamsters an attempt was made to produce lesions by means of alcohol injections. Absolute alcohol (22 microliters) was injected bilaterally, directly into the specific area. All other phases of surgery were the same as described above.

After testing was completed, all the animals were perfused with a 10 percent formalin solution while under deep barbiturate anesthesia. The brains were removed and stored in formalin for at least one week. The brains were frozen and sectioned at 40 microns; every third (in some cases every fifth) section from the beginning to the end of the lesion was mounted on gelatin coated slides and stained with thionin, cresyl violet, or sudan black.

The series of brain sections were examined with the aid of a micro-slide projector and a low power microscope. In each brain the section showing the greatest extent of damage was selected and the area of destruction measured with a planimeter. Since electrolytic lesions tend to be roughly spherical, this measure is proportional to the volume of the tissue actually destroyed.

It was noticed that three rats in experiment I, and two rats in experiment II had distended ventricles, although they had not sustained severe damage to other structures. Such hydrocephalus was not present in the other experimental animals. For each of these hydrocephalic animals, the section in which the lateral ventricles were maximally dilated was selected and the width of the ventricle was measured.

# RESULTS

## I Hoarding Behaviour

Three measures of behaviour in the hoarding situation were obtained for all animals. These were the amount of food hoarded, the number of entrances made into the alley, and the total time spent in the alley (maximum of 25 min./day). Data on all three measures are presented in Tables I to V, but the primary measure used to assess hoarding behaviour was the averaged daily amount of food actually hoarded. This measure was chosen for two reasons: (1) time spent in the alley proved to be a rather complex measure, influenced by activities such as exploration and feeding as well as hoarding, and, (2) the number of entrances made into the alley was closely related to the amount of food actually hoarded. For the group of 30 control animals used in experiment I, the Spearman correlation between amount of food hoarded and number of alley entrances was +.79 ($p < .01$). Even higher correlations were obtained between these measures in many of the brain damaged animal groups.

There were no significant differences between the average amount of food hoarded during the seven day alone or the four day to-gether conditions for either the normal or brain damaged animals. Therefore, the hoarding scores reported are an average of the total 11 days.

Hoarding behaviour in normal rats. Normal rats typically began hoarding food within the first few days of the hoarding test. The behaviour usually began abruptly, a large number of food pellets being hoarded the first day on which at least five pellets (15 gm.) were hoarded (a measure introduced by Morgan, Stellar, & Johnson, 1943). The average time of onset for the 23 naive control animals was the third or fourth day. Ten animals hoarded on days one and two, eight on days three and four, three on the fifth to eight days, and two hoarded nothing during the entire 11 days of the hoarding experiment. The average daily hoard of these naive animals was 36 gm. (range: 0 to 50).

After an animal had begun to hoard it normally continued to hoard at a consistent rate. Individual rats tended to develop a characteristic pattern of behaviour in terms of the time at which they first entered the alley during the 25 min. test period, the speed at which they ran, the amount they hoarded, and the things they did in the alley. Often the rats hoarded all the pellets early in the test period and spent the remaining time exploring the alley, grooming, or sniffing.

All the scores of the control animals are presented in Table I. The behaviour of the seven sham operated rats did not differ signifigantly from that of the naive animals. Therefore the scores for these animals were combined with those of the 23 naive rats so that the total control group consisted of 30 animals who hoarded an average of 33.8 gm. per day.

The effect of brain damage on hoarding. The brain damaged rats from both experiments, as a group, differed from the control rats in several respects. Usually, they spent less time in the alley, made fewer alley entrances, and in general were less active, They frequently dropped the pellets they were carrying to the home cage, and sometimes returned without a pellet. Often, they would eat the pellets at the end of the alley where food had been placed. Control animals were never observed eating in the alley; they always carried the pellets home first.

In addition to such general differences, the brain damaged animals differed from normal in terms of the daily average amount they hoarded. Also, animals with brain lesions in different locations differed from one another.

## TABLE I

## Hoarding Behaviour of Control Animals

## Experiment I

| Animal Number | $\overline{X}$ Hoard (gm.) | $\overline{X}$ Time in Alley (sec.) | $\overline{X}$ Alley Entrances | Hoarding Onset Day |
|---|---|---|---|---|
| Naive Animals | | | | |
| 21 | 40.9 | 413.1 | 14.3 | 2 |
| 22 | 24.8 | 458.9 | 6.3 | 3 |
| 23 | 34.3 | 481.6 | 16.6 | 3 |
| 24 | 46.3 | 794.7 | 19.7 | 2 |
| 25 | 42.3 | 461.9 | 14. | 1 |
| 26 | 4.8 | 15.7 | 1.7 | 11+ |
| 27 | 39.5 | 153. | 10. | 1 |
| 28 | 30.5 | 878.4 | 5.7 | 5 |
| 42 | 29.5 | 121. | 12.9 | 8 |
| 43 | 26.2 | 120.4 | 8.9 | 4 |
| 44 | 43.8 | 282.7 | 15.6 | 3 |
| 45 | 40. | 283.3 | 12.6 | 3 |
| 46 | 42.5 | 291.7 | 18. | 3 |
| 47 | 0 | 6.7 | 3.1 | 11+ |
| 48 | 50. | 390. | 20. | 4 |
| 51 | 45.1 | 371. | 15.9 | 1 |
| 52 | 41.5 | 146.3 | 13.9 | 2 |
| 55 | 48. | 329.7 | 19. | 1 |
| 56 | 50. | 432.7 | 31.6 | 1 |
| 56x | 17.2 | 114. | 10.3 | 5 |
| 57 | 44.4 | 577. | 21.1 | 1 |
| 58 | 45. | 298.9 | 17.9 | 2 |
| 59 | 41.8 | 190.4 | 18.7 | 3 |
| $\overline{X}$ = | 36.1 | 331. | 14.3 | 3.5 |
| Sham Operated Animals | | | | |
| 7 | 42.3 | 229.9 | 15.6 | 3 |
| 8 | 22. | 18.9 | 3.4 | 2 |
| 00 | 4.5 | 28.3 | 3. | 4 |
| 37 | 31.6 | 580.4 | 19.1 | 2 |
| 74 | 21.6 | 58.3 | 8.1 | 2 |
| 93 | 48.6 | 95. | 16.1 | 1 |
| 70 | 14.3 | 106.1 | 6.9 | 10 |
| $\overline{X}$ = | 26.4 | 159.6 | 10.3 | 3.4 |
| Total $\overline{X}$ = | 33.8 | 291. | 13.3 | 3.5 |

## Experiment I

*Hoarding behaviour following section of the mammillothalamic tract.* Examination of the slides revealed that the mammillothalamic tract was sectioned bilaterally in six animals and unilaterally in three. A photomicrograph illustrating unilateral section of the mammillothalamic tract is shown in Figure 2. All six animals with bilateral section of the mammillothalamic tract also had bilateral damage to the mammillary body and to the posterior hypothalamus.

The animals having bilateral damage to the mammillothalamic tract and mammillary body hoarded less food and made fewer alley entrances than any other brain damaged group. The mean amount of food hoarded by these six rats was 5.8 gm., ranging from 0 to 23.4. (See Table II.) This is significantly less than the amount hoarded by the 30 control animals ($p < .001$; Mann-Whitney Test). Only one of the rats with bilateral mammillothalamic tract damage reached the criterion of 15 gm. hoarded in a single day. This rat hoarded on the first testing day.

Although the bilaterally damaged mammillothalamic tract rats failed to hoard, they were not emaciated and actually gained weight while on a food deprivation schedule. The weight change in these animals from before

Fig. 7 Photomicrograph of a coronal brain section showing unilateral section of the mammillothalamic tract, and fornix, together with extensive unilateral damage to the mammillary body and posterior hypothalamus. Sudan black stain. Rat # 89.

## TABLE II
## Effect of Section of the Mammillothalamic Tract on Hoarding Behaviour
## Experiment I

| Animal Number | $\bar{X}$ Hoard (gm.) | $\bar{X}$ Time in Alley (sec.) | $\bar{X}$ Alley Entrances | Hoarding Onset Day | Lesion Size (mm.$^2$) | Additional Structures Damaged |
|---|---|---|---|---|---|---|
| Bilateral section of mammillothalamic tract | | | | | | |
| 84 | 2.3 | 14.9 | .4 | 11+ | 2.53 | mammillary body, fornix, and posterior hypothalamus in all rats |
| 91 | 0 | 0 | 0 | 11+ | 1.96 | |
| 96 | 1. | .1 | .1 | 11+ | 2.20 | |
| 83 | 5.3 | 36.9 | 2.1 | 11+ | 2.09 | |
| 82 | 23.4 | 14.9 | 4.9 | 1 | .77 | |
| 81 | 2.8 | 468.7 | 1.5 | 11+ | 2.98 | |
| $\bar{X}$ = | 5.8 | 89.3 | 1.5 | 9.3 | 2.09 | |
| Unilateral section of mammillothalamic tract | | | | | | |
| 89 | 48.9 | 257.7 | 17.4 | 1 | 1.96 | fornix & mammillary |
| 97 | 7.7 | 13.3 | 2.4 | 7 | 1.37 | " body |
| 95 | 13.7 | 31. | 3.4 | 2 | .97 | fornix (unilateral) |
| | 23.4 | 100.7 | 7.7 | 3.3 | 1.43 | mammillary body & thalamus |

surgery to the period after all testing was completed, was a slight gain of 6.0 gm. (ranging from no change in two animals, to a 15.0 gm. gain in one animal). The control animals, over the same period, showed a slight average weight loss of 5.1 gm. However, the animals with bilateral mammillothalamic tract and mammillary body damage did consume less food than the control animals during the daily 25 min. hoarding test period. The control rats ate an average of 5.8 gm. (ranging from 2.3 to 10.6) while the six brain damaged rats ate an average of 2.3 gm. (ranging from 0 to 7). This was a significant difference ($p < .01$; Mann-Whitney Test).

All six rats having bilateral section of the mammillothalamic tract and damage to the mammillary body had also sustained bilateral section of the fornix. In three cases the thalamus had been injured as well. It appears likely that such incidental damage to the fornix or thalamus is not responsible for the severe deficits observed in hoarding behaviour and that either section of the mammillothalamic tract or destruction of the mammillary body is the crucial factor. First, two animals had sustained moderate ventromedial thalamic damage and one had a large medial thalamic lesion destroying the dorsal medial nucleus, the intralaminar and mid-line nuclei and the habenula. These three animals hoarded as well as the three in which the thalamus was intact. Also, seven rats to be reported below (see page 29) had extensive thalamic damage yet hoarded significantly more than the bilaterally damaged mammillothalamic tract group ($p < .004$; Mann-Whitney Test).

Fornix section was probably not crucial either. Two animals had sustained bilateral section of the fornix but only unilateral section of the mammillothalamic tract. In one of these cases the mammillary body had been damaged unilaterally as well. One animal hoarded an average of 7.7 gm. per day; the other, hoarded 48.9 gm. per day. Another animal which had unilateral section of the mammilothalamic tract and fornix with bilateral damage to the mammillary body and thalamus hoarded an average of 13.7 gm. Only one of the six rats with bilateral section of the mammillothalamic tract hoarded more than 6 gm. per day.

In addition, four animals (rats no. 4, 11, 34, from Table III; and rat no. 22 from Table V) were found in which the fornix was severely damaged at the level of the anterior commissure (these animals also had septal and thalamic damage.) Only one of these four animals was a poor hoarder. Their average hoard was 18.2 gm. (range: 11.2 to 26.7 gm.). When the hoarding behaviour of the seven animals (two with bilaterally sectioned fornix and unilateral damage to the mammillothalamic tract, one with unilaterally sectioned fornix and unilateral mammillothalamic tract damage, and the four rats with the fornix bilaterally damaged at the level of the anterior commissure) as a group, were compared to the hoarding of the six rats with bilateral mammillothalamic tract section and damage to the mammillary body, there was a significant difference ($p < .02$; Mann-Whitney Test). Thus, the evidence suggests that section of the mammillothalamic tract produces a greater depression of hoarding behaviour than does section of the fornix.

However, all animals with bilateral lesions of the mammillothalamic tract and mammillary body also sustained damage to the posterior hypothalamus. It is possible that such damage is partially responsible for the deficits observed in hoarding behaviour, eventhough the damage tended to be slight and its extent did not appear to be correlated with the amount of food hoarded, since it is well known that damaging the lateral hypothalamus results in aphagia (Teitlebaum & Epstein, 1962).

It is unlikely that the poor hoarding performance of the animal with bilateral mammillothalamic tract and mammillary body damage was related to the extent of brain damage in an absolute sense. Table II gives the

the extent of destruction in a section passing through the center of the lesion in these animals. The average area measured in this way was 2.09 mm.$^2$, ranging from .77 mm.$^2$ to 2.98 mm.$^2$ This measure of damage did not correlate with the amount of food that the six rats hoarded. The extent of damage for the seven animals with fornix damage (but no bilateral mammillothalamic tract or mammillary body damage) as measured through the center of the lesion averaged 2.41 mm.$^2$ (range: .97 mm.$^2$ to 4.05 mm.$^2$). The difference between the two groups is not significant. Therefore, it is clear that lesions size per se is not a critical factor in the poor hoarding performance of the rats with mammillothalamic tract damage.

Effect of thalamic damage on hoarding behaviour. Hoarding scores for the seven animals that sustained thalamic damage are presented in Table III. The locus of damage varied considerably from one animal to another. In two cases there was extensive damage to the anterior and medial thalamus that extended caudally into the mid-brain. In another animal there was unilateral medial and unilateral lateral damage to the thalamus with damage also to the habenula. The remaining four animals had small bilateral lesions.

## TABLE III
## Hoarding Behaviour Following Brain Damage not involving the Mammillothalamic Tract

| Animal Number | $\overline{X}$ Hoard (gm.) | $\overline{X}$ Time in Alley (sec.) | $\overline{X}$ Alley Entrances | Hoarding Onset Day | Lesion Size (mm.$^2$) | Additional Structures Damaged |
|---|---|---|---|---|---|---|
| Damage to the Thalamus | | | | | | |
| 6 | 13.4 | 42.3 | 4.3 | 2 | 6.85 | anterior thalamus |
| 71 | 33.4 | 130. | 12.9 | 1 | .65 | habenula |
| 72 | 31.7 | 82.9 | 13.3 | 3 | 1.02 | |
| 73 | 23. | 101.3 | 12. | 3 | 1.70 | |
| 75 | 36.2 | 232.1 | 16.9 | 2 | 1.85 | |
| 76 | 32. | 483.1 | 16.7 | 3 | 1.30 | |
| 87 | 26. | 87.6 | 13.4 | 3 | 5.38 | |
| $\overline{X}$ = | 27.9 | 165.6 | 12.8 | 2.4 | 2.68 | |
| Damage to the Septum | | | | | | |
| 3 | 13.4 | 15. | 3. | 3 | 6.48 | Anterior thalamus |
| 4 | 13.4 | 13. | 3.1 | 11 | 2.22 | |
| 34 | 11.2 | 3.7 | 1.4 | 2 | 3.89 | preoptic area |
| 62 | 16.2 | 53.4 | 8.3 | 9 | 1.02 | |
| 63 | .4 | 31. | 5.9 | 11+ | .99 | |
| 61 | 25.7 | 263.7 | 16.6 | 7 | 1.04 | |
| 32 | 25. | 56. | 10.9 | 2 | .74 | |
| $\overline{X}$ = | 15. | 62.3 | 7. | 6.4 | 2.34 | |
| Damage to the Hippocampus | | | | | | |
| 64 | 38.8 | 227.2 | 17.1 | 3 | 2.53 | |
| 65 | 44. | 330.9 | 21.4 | 1 | 2.59 | unilateral lesion |
| Hydrocephalus | | | | | | |
| 11 | 21.6 | 30.3 | 6. | 2 | 4.05 | |
| 36 | 47.4 | 118.6 | 15.3 | 1 | .39 | unilateral septum |
| 66 | 36.1 | 88.6 | 17.4 | 5 | 2.65 | hippocampus & unilateral thalamus |
| $\overline{X}$ = | 35. | 79.2 | 12.9 | 2.7 | 2.36 | |

The average lesion size as measured through the center of the lesion was 2.68 mm.$^2$ A photomicrograph illustrating an anterior thalamic lesion is presented in Figure 3.

The mean daily amount of food hoarded for this group was 27.9 gm. (range: 13.4 to 36.2). This was not significantly different from the 30 control animals ($p < .17$; Mann-Whitney Test) but was significantly greater than the six bilaterally damaged mammillothalamic tract rats ($p < .004$; Mann-Whitney Test). There was no significant difference in the absolute size of the brain lesions in these two brain damaged groups.

*Effect of septal and hippocampal damage on hoarding behaviour*. The septal nuclei were moderately to severely damaged in seven rats. A representative section through the center of the lesion in one animal is illustrated in Figure 4. The septal damaged rats as a group hoarded an average of 15 gm. (range: .4 to 25.7). (See Table III.) This performance was inferior to that of the 30 control animals ($p$ .002; Mann-Whitney Test), but they tended to hoard more than the six animals with bilateral mammillothalamic tract damage ($p < .10$). There was no significant difference in absolute lesion size between the latter two groups.

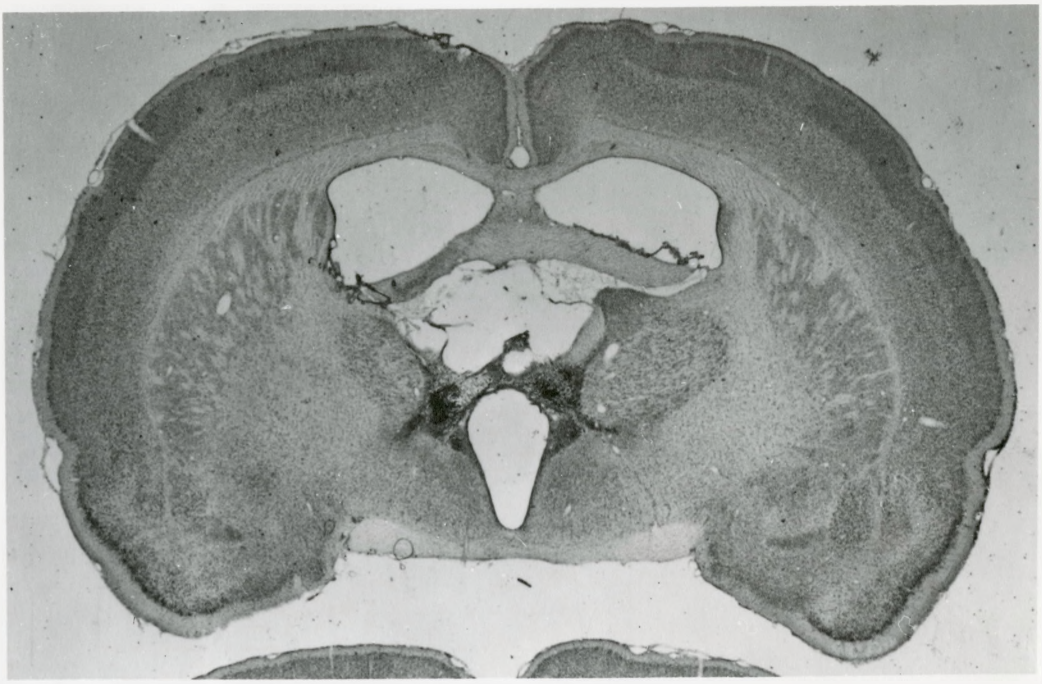


Fig. 3 Photomicrograph of a coronal brain section showing bilateral anterior thalamic damage partially sparing n. anterior dorsalis and n. anterior ventralis on one side. Cresyl violet stain. Rat # 87.

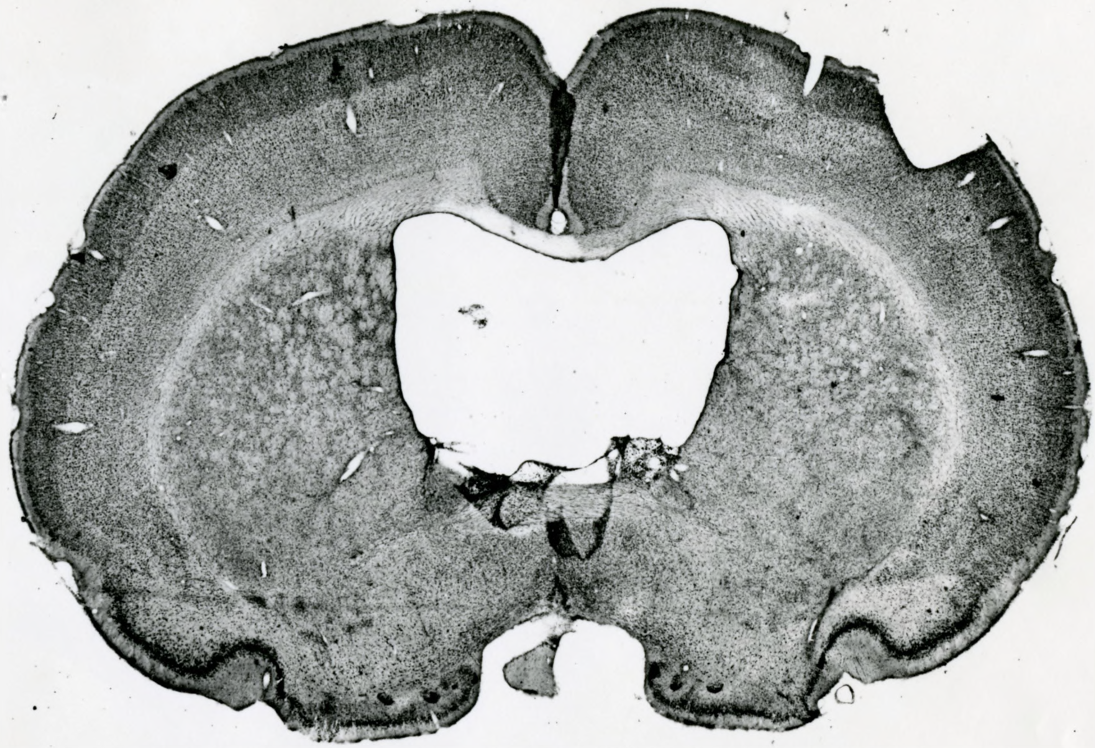


Fig. 4 Photomicrograph of a coronal brain section showing a representative bilateral septal lesion. Thionin stain. Rat # 3.

Two animals received hippocampal lesions. A photomicrograph is presented in Figure 5. Although their lesions were relatively large (2.53 mm.$^2$; 2.59 mm.$^2$) their average hoard was quite high at 38.8 and 44. gm. This observation that normal hoarding behaviour is possible in the presence of extensive hippocampal destruction is consistent with the previous finding that section of the fornix does not have a severe effect on hoarding.

*Effect of hydrocephalus on hoarding.* Three animals in experiment I were found to have distended ventricles (hydrocephalus) eventhough they had only small brain lesions. One animal had fornix column damage, another had a small unilateral septal lesion and the third had slight hippocampal and unilateral thalamic damage. Despite the severity of the hydrocephalus (see Figure 6) their average hoard of 35 gm. (range: 21.6 to 47.4) was well within the range of the control animals.

### Experiment II: Hoarding test before and after surgery

Experiment II consisted of 22 animals. Before sham surgery the control group of ten rats hoarded an average of 36.4 gm. and after the recovery period they had an average daily hoard of 47.5 gm. (range: 40.6 to 50). (See Table IV.) Of the remaining 12 animals, five had

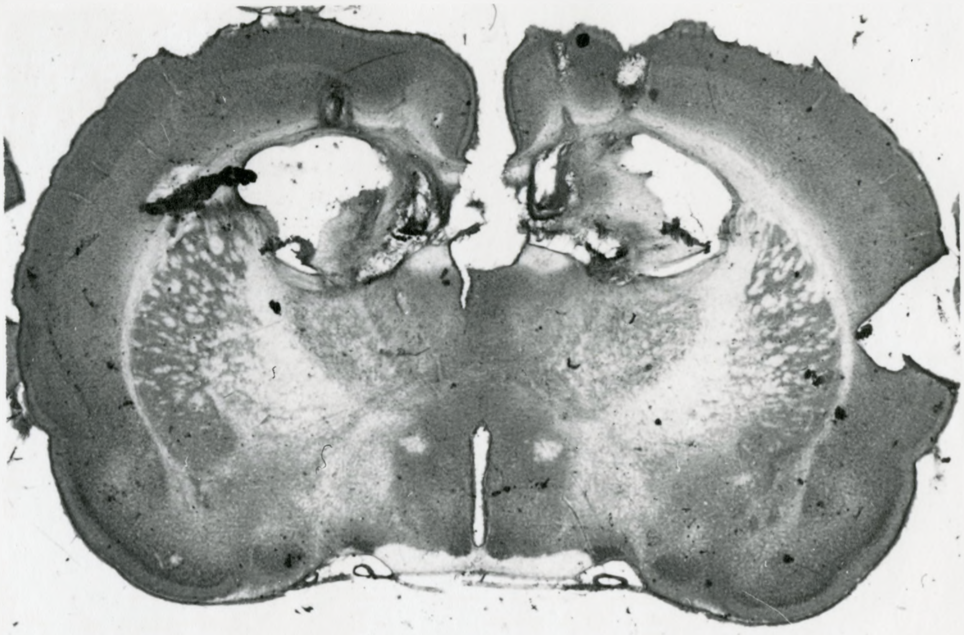


Fig. 5 Photomicrograph of a coronal brain section showing bilateral hippocampal damage. Cresyl violet stain. Rat # 64.

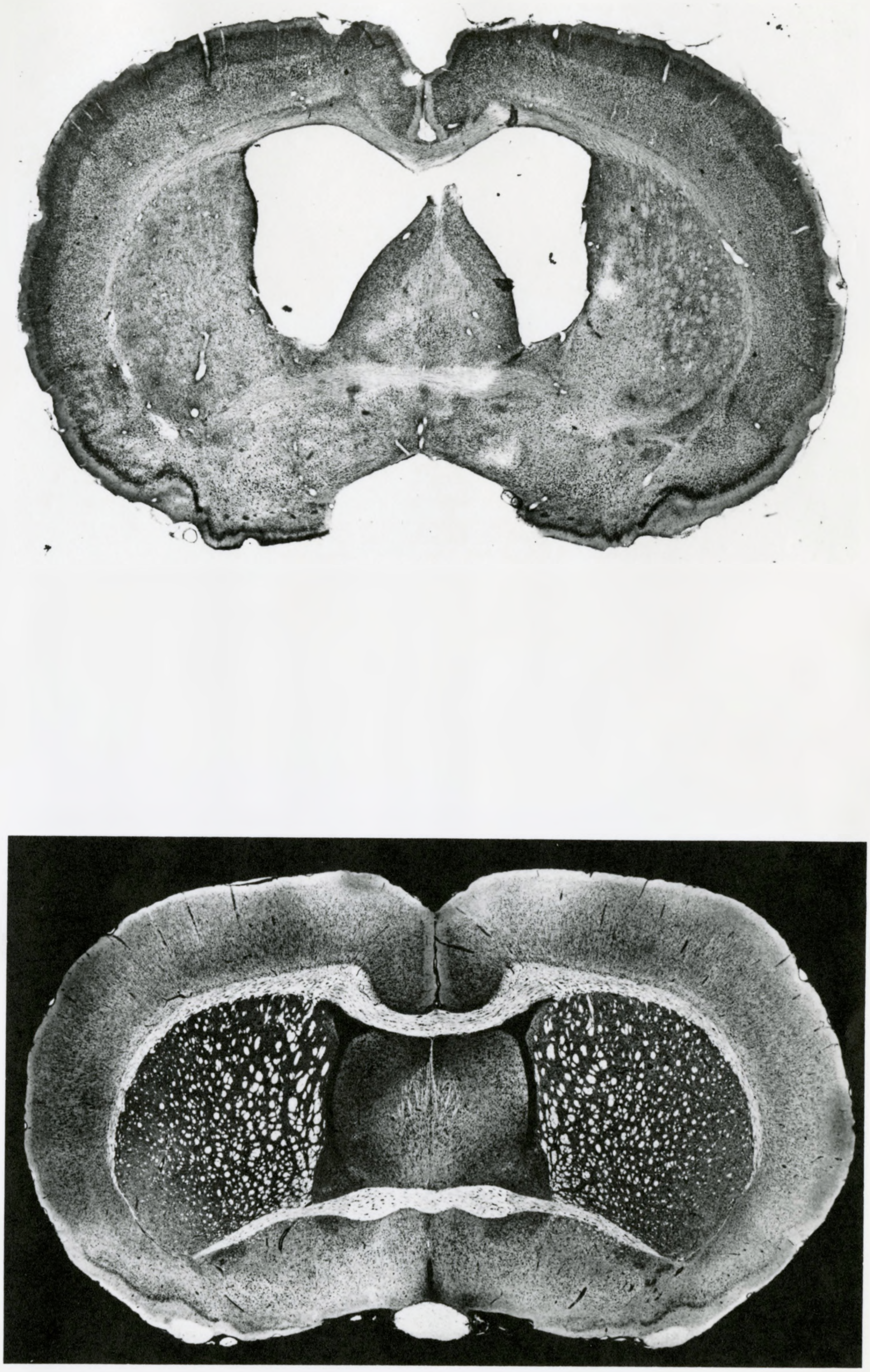


Fig. 6 Photomicrograph of a coronal brain section (cresyl violet stain) showing hydrocephalus and a comparable normal section from Konig and Klippel (1963).

## TABLE IV
## Hoarding Behaviour of Control Animals
## Experiment II (second test series-following surgery)

| Animal Number | $\bar{X}$ Hoard (gm.) | $\bar{X}$ Time in Alley (sec.) | $\bar{X}$ Alley Entrances | Hoarding Onset day |
|---|---|---|---|---|
| 24 | 50. | 268.5 | 17.7 | 1 |
| 25 | 50. | 106.2 | 16. | 1 |
| 44 | 42.5 | 244.6 | 9. | 1 |
| 48 | 50. | 276.7 | 17. | 1 |
| 57 | 50. | 669.9 | 31.3 | 1 |
| 59 | 50. | 197.4 | 21.9 | 1 |
| 42 | 50. | 136. | 16. | 1 |
| 43 | 40.6 | 31.3 | 2. | 1 |
| 45 | 43.8 | 181.7 | 12. | 1 |
| 47 | 48.5 | 87.7 | 15. | 2 |
| $\bar{X}$ = | 47.5 | 220. | 15.8 | 1.1 |

septal lesions, three had hippocampal damage, two sustained thalamic damage and two were hydrocephalic.

The onset of hoarding (15 gm. criterion) in the control animals before sham surgery occurred, on the average, on day 4. After surgery hoarding began on day 1. The brain damaged animals began hoarding on day 3 before surgery and on the second and third days after surgery. Both of these changes in time of onset were significant ($p < .01$; Wilcoxon Test). The mean daily hoard for the brain damaged animals after surgery was 40.4 gm. which was not significantly different from the control animals' hoard of 47.5 gm. (Mann-Whitney Test). (See Table V.) Thus, the two groups appear identical. However, the brain lesions may have had a slight effect on retention of established hoarding behaviour. The control animals hoarded an average of 36.4 gm. of food prior to surgery and 47.5 gm. afterwards. This increase is significant ($p < .01$; Wilcoxon Test). The brain damaged animals also showed a slight increase in amount of food hoarded (35.4 gm. before surgery and 40.4 gm. afterwards) but the change was not significant.

Since experiment I had shown that septal lesions retarded the acquisition of hoarding behaviour, the data

# TABLE V
## Hoarding Behaviour Following Brain Damage
## Experiment II

| Animal Number | $\bar{X}$ Hoard (gm.) | $\bar{X}$ Time in Alley (sec.) | $\bar{X}$ Alley Entrances | Hoarding Onset Day | Lesion Size (mm.$^2$) | Additional Structures Damaged |
|---|---|---|---|---|---|---|
| Damage to the Thalamus | | | | | | |
| 21 | 43.4 | 174.2 | 16.7 | 1 | 3.03 | anterior thalamus |
| 52 | 48.5 | 116.4 | 20.6 | 2 | .56 | |
| Damage to the Septum | | | | | | |
| 28 | 9.5 | 193. | 2.5 | 8 | 1.94 | caudate |
| 23 | 26.4 | 39. | 7.7 | 1 | .19 | unilateral fornix |
| 56 | 50. | 381.1 | 36.4 | 1 | .39 | caudate |
| 56x | 49.5 | 227.4 | 22.4 | 5 | .30 | |
| 58 | 50. | 197.4 | 21.9 | 2 | .65 | |
| $\bar{X}$ = | 37.1 | 207.6 | 18.2 | 3.4 | .69 | |
| Damage to the Hippocampus | | | | | | |
| 46 | 50. | 517.3 | 23. | 1 | .65 | unilateral lesion |
| 51 | 48.9 | 120.6 | 19.9 | 1 | 3.15 | |
| 55 | 45.9 | 143.7 | 17.4 | 1 | 1.63 | " thalamus |
| $\bar{X}$ = | 48.3 | 260.5 | 20.1 | 1 | 1.81 | |
| Hydrocephalus | | | | | | |
| 22 | 26.7 | 83. | 11.3 | 1 | | anterior thalamus |
| 26 | 35.6 | 29. | 5.7 | 6 | | preoptic area & n. reuniens |

of the five septal-damaged rats in experiment II were examined separately. The results were similar to those of the total group of brain damaged animals. Septal damage did not result in a significant loss of retention of hoarding behaviour. However, it cannot be concluded from this that septal damage affects acquisition of hoarding only, with no effect on retention, because the lesions in the two experiments differ in size. The average extent of septal damage in experiment I was 2.3 mm.$^2$; in experiment II it was 0.7 mm.$^2$ This difference is significant ($p < .03$; Mann-Whitney Test).

## Nest Building Experiment

After the last hoarding test day, all rats were tested on nest building.

Control animals. All naive and sham operated rats seemed to discover the string hanging from their cage ceiling almost immediately, and within an hour, built a nest by pulling down the string. They usually used enough string to build a nest that half filled the bottom of their cage and was three to four inches deep. They chewed the string into short pieces and then fluffed it with their teeth. A curious fact was that most nests were built close to the water spout.

Brain damaged animals. Of all the tests given to the brain damaged animals, nest building showed the least difference from the behaviour of control animals. Only one animal out of both experiments I and II failed to build a nest and it had one of the most severely damaged brains. There was extensive damage to the medial and lateral thalamus, hippocampus, plus massive hydrocephalus. Four animals however, built very small nests. One of these rats sustained anterior thalamic and medial thalamic damage; one septal damage and hydrocephalus; one bilaterally damaged septum; and one a bilaterally damaged hippocampus. All other rats, even those with a bilateral mammillothalamic tract damage, built medium sized nests. The persistance of nest building in brain damaged animals is a surprising result since it involves many of the complex behaviours used in food hoarding.

## Avoidance Experiment

After the nest building test was completed, all rats in experiments I and II were tested on the one-way avoidance task. Unfortunately, part of the data were lost and results are available for only 15 control rats and 35 brain damaged rats. (See Table VII.) These groups include animals from both hoarding experiments.

In general, the results indicate that in the brain

## TABLE VI
## Avoidance Behaviour in Control and Sham Operate Rats

| Animal Number | Experiment | $\bar{X}$ Hoard (gm.) | $\bar{X}$ Shocks Received |
|---|---|---|---|
| 7 | 1 | 42.3 | 9 |
| 8 | 1 | 22. | 11 |
| 00 | 1 | 4.5 | 5 |
| 37 | 1 | 31.6 | 3 |
| 74 | 1 | 21.6 | 7 |
| 93 | 1 | 48.6 | 5 |
| 70 | 1 | 14.3 | 6 |
| 24 | 2 | 50. | 6 |
| 25 | 2 | 50. | 30 |
| 44 | 2 | 42.5 | 9 |
| 48 | 2 | 50. | 3 |
| 42 | 2 | 50. | 5 |
| 43 | 2 | 40.6 | 6 |
| 45 | 2 | 43.8 | 2 |
| 47 | 2 | 48.5 | 4 |

## TABLE VII
## Effect of Brain Damage on Avoidance Behaviour

| Animal Number | Experiment | $\overline{X}$ Hoard (gm.) | $\overline{X}$ Shocks Received | Structures Damaged |
|---|---|---|---|---|
| 84 | 1 | 2.3 | 22 | mammillothalamic tract & mammillary body, fornix, posterior hypothalamus |
| 91 | 1 | 0 | 30 | |
| 96 | 1 | 1. | 30 | |
| 83 | 1 | 5.3 | 30 | " |
| 82 | 1 | 23.4 | 14 | " |
| 81 | 1 | 2.8 | 30 | " |
| | | | $\overline{X}$ =26. | |
| 89 | 1 | 48.9 | 6 | mammillothalamic tract (unilateral) |
| 97 | 1 | 7.7 | 11 | |
| 95 | 1 | 13.4 | 6 | " |
| | | | $\overline{X}$ =7.7 | |
| 3 | 1 | 13.4 | 28 | septum |
| 4 | 1 | 13.4 | 15 | " |
| 34 | 1 | 11.2 | 23 | " |
| 62 | 1 | 16.2 | 9 | " |
| 63 | 1 | .4 | 7 | " |
| 61 | 1 | 25.7 | 6 | " |
| 32 | 1 | 25. | 19 | " |
| 28 | 2 | 9.5 | 23 | " |
| | | | $\overline{X}$ =16.3 | |
| 6 | 1 | 13.4 | 30 | thalamus |
| 71 | 1 | 33.4 | 6 | " |
| 72 | 1 | 31.7 | 2 | " |
| 73 | 1 | 23. | 6 | " |
| 75 | 1 | 36.2 | 4 | " |
| 76 | 1 | 32. | 6 | " |
| 87 | 1 | 26. | 10 | " |
| 21 | 2 | 43.4 | 14 | " |
| 52 | 2 | 48.5 | 8 | " |
| | | | $\overline{X}$ = 9.6 | |
| 64 | 1 | 38.8 | 8 | hippocampus |
| 65 | 1 | 44. | 4 | " |
| 46 | 2 | 50. | 4 | " |
| 51 | 2 | 48.9 | 4 | " |
| | | | $\overline{X}$ = 5. | |
| 11 | 1 | 21.6 | 25 | hydrocephalus |
| 36 | 1 | 47.4 | 5 | " |
| 66 | 1 | 36.1 | 18 | " |
| 22 | 2 | 26.7 | 24 | " |
| 26 | 2 | 35.6 | 7 | " |
| | | | $\overline{X}$ =15.8 | |

damaged group, rats that hoarded poorly made few avoidance responses. When the average amount of food hoarded was correlated with the number of shocks received for all the 35 brain damaged animals, $r = -.64$ ($p < .001$; Spearman Rank Correlation Coefficient). The six rats with bilateral mammillothalamic tract damage hoarded less food than any other group; they were also the poorest avoiders, receiving an average of 26 shocks on the test. This level of performance is inferior to that of the control rats ($p < .002$; Mann-Whitney Test). According to the results of the hoarding experiments, septal damage also interferes with hoarding behaviour, though to a lesser extent than mammillothalamic tract damage.

None of the other brain damaged groups differed significantly from the control rats in avoidance behaviour.

Severe hydrocephalus may have an adverse effect on avoidance behaviour. The group of five rats with enlarged ventricles received an average of 15.8 shocks which is more than twice the average of the control rats. The difference between the groups, however, is not significant statistically (Mann-Whitney Test).

There was no relation between avoidance performance and amount of food hoarded in the control rats (Spearman Rank Correlation Coefficient = 0.08).

## Hamster Experiment

Seven naive hamsters were tested in the rat hoarding cages. Although left on ad libitum food, these hamsters hoarded all the 50 grams of food available every day starting on the first test day. No animal ever left any pellets remaining in its alley. They also appeared to be more active than the rats, probably because their movements were very quick. Hamsters usually carried two or three pellets at a time, stuffing them into the pouches in their cheeks. During some pilot testing it was found that they would hoard anything left for them including lettuce, large cotton balls, carrot sticks, orange peels, and pencils.

Since there was such great consistency in hoarding in the hamsters, the hoarding test before surgery was eliminated. Seven hamsters received electrolytic lesions. Again, after surgery, all of these animals hoarded all the pellets available on <u>every</u> day. Their brain damage however was slight, and involved the septum, or hippocampus, or thalamus.

Since it was observed that the hamsters still were more active than rats even after surgery, a sample of four animals' activity was taken for seven days. The mean time in the alley was 560.2 sec. (range: 341 to 916.2) which was much longer than most rats spent ($\overline{X}$. 291.1 sec.), yet they made only 7.1 runs (range: 5.2 to 10.2) which was comparable to the average number of runs made by control rats ($\overline{X} = 13.3$). (See Table VIII.) The reason for this was that the hamsters were able, by taking several pellets at a time, to complete their hoarding in six or seven runs. The rest of the time in the alley was spent in running up and down but no re-entering their home cage, thus yielding a high score for the length of time spent in the alley but a low score for the number of runs to the home cage.

Thus the most interesting result of the hamster experiment was the discovery of the regularity and consistency of food hoarding and its persistance after brain damage.

### TABLE VIII
### Hamster Hoarding Test After Surgery

| | $\overline{X}$ Hoard (gm.) | $\overline{X}$ Time in Alley | $\overline{X}$ Alley Entrances |
|---|---|---|---|
| | 50 | 341. | 5.7 |
| | 50 | 600.5 | 7.3 |
| | 50 | 383. | 5.2 |
| | 50 | 916.2 | 10.2 |
| $\overline{X}$ = | 50 | 560.2 | 7.1 |

## DISCUSSION

The main finding of this thesis was that bilateral damage involving the mammillothalamic tract, mamillary body, and posterior hypothalamus causes a severe depression of hoarding. A less severe depression was found in rats with damage to the septum. Hoarding seemed relatively unaffected by damage to the fornix, thalamus, hippocampus, or damage caused by hydrocephalus. Hoarding was also independent of the size of the lesion.

Previously, Stamm (1955b) had found that ablation of the median cortical strip including the cingulate gyrus severely impaired hoarding behaviour, and recently Vanderwolf (1966) found subnormal hoarding resulted from injury to the anterior thalamus. The present experiment did not confirm this result. However, only three animals sustained anterior thalamic damage and destruction was not complete in any animal. The lesion in the rat having the most extensive anterior thalamic damage is illustrated in Figure 3. Smaller lesions were found in the other two animals. The studies of Stamm and Vanderwolf plus the results of this thesis suggest that there may be a circuit for hoarding involving the mammillary body, the mammillothalamic tract, the anterior nuclei of the thalamus and then by the projections of the medial thalamocortical radiations to the cortex of the cingulate gyrus. The hippocampal formation and fornix appear less important but the septal nuclei do appear to play a role in hoarding behaviour. Therefore, although the results are somewhat puzzling from an anatomical point of view (since the septal nuclei and the hippocampal formation are extensively interconnected) it appears that only some of the structures of the circuit proposed by Papez are involved in hoarding. Similar circuits involving specific modified pathways of Papez circuit have been proposed for drinking behaviour (Fisher & Coury, 1962) and for penile erection (MacLean & Ploog, 1962).

The decrease in hoarding that was found in the animals with bilateral mammillothalamic tract and mammillary body damage was paralleled by deficits in other behaviour. They were very hypoactive, making few entrances into the alley and spending little time there when they did. The depressed hoarding might therefore be due to their general inactivity or perhaps to some change in their emotionality. It has been shown that rats tend to hoard when their alleys are unfamiliar and when their cages have been established as a familiar home area (Miller & Viek, 1944). Perhaps these brain damaged rats failed to establish such territoriality. The bilaterally damaged mammillothalamic tract and mammillary body animals were also severely impaired in learning the one-way avoidance task. Previously, Thomas, Fry, Fry, Slotnick & Krieckhaus (1963) and Krieckhaus (1965, 1966a, 1966b) had also found avoidance deficits (using a shuttle box) in cats and rats with mammillothalamic tract lesions.

Poor avoidance performance was also shown by animals with extensive septal damage. Previously, Kenyon (1962) had reported that septal damage interfered with one-way avoidance performance.

Although there was no correlation between the amount of food hoarded and the number of shocks received during the acquisition of the avoidance response in control rats, there was a significant negative correlation found in all the brain damaged animals as a group. This suggests that hoarding and avoidance behaviour depend on a common central mechanism. In common sense terms one could say that all the animals were generally deteriorated and that a wide variety of behaviours were adversely affected.

The results of the nest building experiment in which only one rat out of all the rats tested failed to build a nest, raised a new important question. Why did animals who failed to hoard food, later build satisfactory nests? This is puzzling as many of the same behaviours are involved, for example: approaching the food pellets and approaching the string; picking up the pellets and biting off the string; returning with the pellets and piling the strings into a nest. There are several possible explanations. There might have been a specific loss in food motivation so that the rats would build nests or engage in activities not related to food. This hypothesis was supported by the finding that the bilaterally damaged mammillothalamic tract and mammillary body animals consumed significantly less food during the test period than the control rats. It is unlikely that fear of entering the alley was an important factor for the nonhoarders since the operated animals were quite tame. Perhaps less actual motor effort was required in building a nest as compared to running down to the end of the alley and carrying back a pellet. Another possibility is that the string was easily accessible and constantly available for 24 hours as compared to the relatively short 25 minute period allotted for food hoarding. Since the nest building test always followed the hoarding test there might have been some effect of order. The experiment did not provide any information about this possibility.

Many incidental observations were made throughout the experiments. The general characteristics of hoarding behaviour were remarkably similar in both the control animals and the brain damaged animals as a group. Stamm (1955) was also impressed by the persistance of the hoarding pattern even after his rats had received very large (29 to 59 percent) cortical lesions. He also observed a sudden onset of hoarding in both control and brain damaged animals.

An unexpected finding was that eventhough animals did not always hoard all the food available the amount hoarded seemed to be related to the quantity of hoarding material present. Excluding the animals who hoarded 50 gm. when 50 gm. were available, all other animals, including control and brain damaged rats, hoarded more than their previous average hoarding on the single test day when 150 gm. were available. A contributing factor to this potentiation might have been that the 150 gm. test day was always the last of the hoarding tests when the rats had had maximum experience. This variable of practice, at least during the period before surgery, was found to increase the hoarding performance of the control animals after sham surgery, but did not increase the hoarding level of the brain damaged animals. Stamm (1955) also found that hoarding experience before surgery had no effect on the hoarding behaviour of rats after they had received large cortical ablations.

The condition of hoarding alone in a room, or hoarding in the presence of other rats, was not found to affect the amount of pellets hoarded for either the control or brain damaged rats. Previous investigators (Denenberg, 1952; Miller & Postman, 1946; Ross, Smith & Denenberg, 1950) did find that there was social facilitation of eating under group conditions and that this interfered with hoarding behaviour. However, the social conditions of this experiment did not involve physical contact among the rats, which might have been a crucial factor in the results of the other experiments.

One observation that was made only with brain damaged animals was that they frequently dropped their food pellets along the alley before they reached their home cage. This might be compared to Stamm's (1955) description of the unorganized behaviour of female rats that had received median cortical damage. If an air blast destoyed their nests they would not reconstruct them but would run aimlessly around the compartment picking up and randomly dropping the paper strips. Perhaps such incomplete sequencing of events is a general result of limbic system intervention, as Pribram (1960) has suggested.

The generality of the results of the rat experiments failed to be applicable to another species, the golden Syrian hamster. First of all, nondeprived unoperated hamsters always hoarded all the pellets (50 gm.) on the first day that they were available, and continued to hoard all pellets on all the following test days. Waddell (1951) who first investigated hoarding in the hamster in the laboratory, estimated that in terms of body weight, food satiated hamsters hoarded approximately 4½ times more food than rats. Secondly, although they hoarded a maximum amount before surgery and were also very active, this continued <u>without change</u> after surgery.

Only one previous study had explored the effect of subcortical damage on hoarding in hamsters. Bunnell, Sodetz, & Shalloway (unpublished, 1966) found that hamsters with large bilateral septal damge no longer hoarded food, nor built nests, and were hypoactive. Their observations were made over an eight month period thus suggesting that the effects were permanent. Although the hamsters in this experiment did sustain septal and hippocampal damage (but none to the mammillothalamic tract or mammillary body) the septal lesions reported by Bunnell were much more extensive. Perhaps if the lesions of this experiment had been larger, some change in hoarding behaviour would have occurred. It may be more difficult to disrupt hoarding in hamsters than in hooded rats.

# SUMMARY

The effects of subcortical electrolytic brain damage on food hoarding, nest building, and avoidance behaviour were studied in rats. Brain damaged hamsters were tested only on food hoarding. It was found that:

1. Rats with bilateral damage to the mammillothalamic tract, mammillary body, and posterior hypothalamus were inactive, ate less than normal, hoarded very little food and performed poorly on an avoidance task. Septal damage had similar, but less severe effects. Other rats with damage to the thalamus, hippocampus, fornix, fornix columns, behaved more nearly like control animals.

2. A hoarding circuit is proposed involving the mammillary body and mammillothalamic tract, the anterior nuclei of the thalamus and cortex of the cingulate gyrus.

3. In brain damaged animals, the amount of food hoarded correlated with the activity level of the rats and the number of shocks they received during the avoidance task. Hoarding was not found to be affected

by the presence or absence of other rats or by the absolute size of the lesion.

4. Only one brain damaged rat failed to build a nest.

5. Syrian hamsters are more active, hoard more food pellets, and show greater persistance of hoarding after brain damage than do hooded rats.

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