

ALTERED FOOD PREFERENCES AFTER LESIONS IN THE BASOLATERAL REGION OF THE AMYGDALA IN THE RAT¹

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Rats with lesions in the basolateral amygdala chose different foods from control rats in 10-min. food-preference tests. The normal rats ate primarily familiar chow, while the amygdala-lesioned rats ate primarily novel foods. The lesioned rats did not select indiscriminately but showed definite preferences. With repeated testing, the normal rats' preferences became similar to those of the amygdala-lesioned rats. Food-preference tests in a disturbing environment suggested that the difference between the lesioned and control groups was not due to a general alteration in behavior such as fear. Other aspects of ingestive behavior, such as body weight regulation, were not primarily altered by the lesions. The basolateral amygdala may therefore be concerned with the selection of foods on the basis of previous experience.

Amygdaloid neurons are activated in eating and drinking elicited by electrical stimulation of the lateral hypothalamus in rats (E. T. Rolls, 1972). This indication that amygdaloid neurons are involved in eating and drinking is strengthened by the finding that the amygdaloid neurons directly excited by the stimulation have the same absolute refractory period as the neurons through which the eating and drinking are elicited (E. T. Rolls, 1973). To investigate further the role of the amygdala in eating, ingestive behavior following amygdaloid lesions was analyzed, as described here. The lesion electrodes were aimed at the basolateral region of the amygdala, which is the area in which neurons were activated in the electrically elicited eating and drinking (E. T. Rolls, 1972).

Electrophysiological and behavioral studies (see E. T. Rolls, 1972) support the hypothesis that the amygdala is involved in reinforcement. This hypothesis was utilized in the experiments described here. A choice of foods was given to the lesioned animals to determine whether the reward value of different foods measured by food preference is altered by the lesions.

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GENERAL METHOD

Subjects

Sixty-six male hooded Lister rats and 13 male albino Wistar rats weighing 250-300 gm. at the start of the experiments were divided randomly into an experimental group of 60 animals and a control group of 19 animals.

Apparatus

Food-preference tests were conducted in a wire-mesh rat cage with the dimensions indicated in Figure 1. Six different foods, arranged for Experiment 1 as in Figure 1, were placed in black plastic bottle tops 6 cm. in diameter. Each food cup contained about 5 gm. of chopped food. The rat cage was placed on a table in a small room.

Procedure

The rats were maintained in individual cages with ad-lib water. Standard laboratory chow in pellet form—Dixon's FFG(M)—was available in hoppers or on the floor of the cage. On the day before a food-preference test the food was removed at 1530, 2½ hr. before the lights were extinguished (illumination was off between 1800 and 0800).

For a food-preference test, a rat was deprived of food overnight and tested in the morning. Often the experimenter did not know whether the subjects were control or experimental animals. A stopwatch was started when the rat was placed in the cage, and the time when a rat started and stopped eating each type of food was noted. Eating was defined as picking up food, biting and chewing it, and ingesting it. After 10 min. the rat was removed from the cage, and the times spent eating each type of food were determined. Laboratory chow was given to the animal much later, in the afternoon. A rat was tested only once a day with a minimum of 2 days between tests.

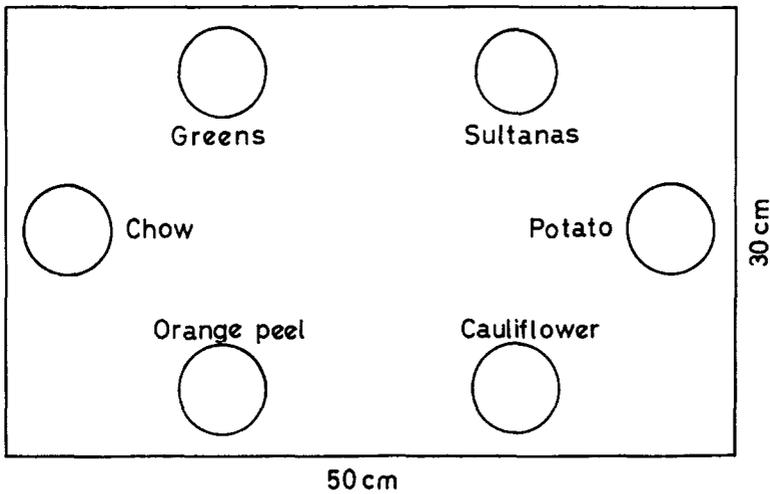


FIG. 1. Plan of arrangement of foods in the wire-mesh test cage. (Each food was in a container 1.0 cm. high.)

Surgery

Bilateral lesions were made in the region of the basolateral amygdala of the experimental group of rats.

The rats were anesthetized with an intraperitoneal injection of 3 ml/kg of Equi-Thesin (Jensen-Salsbury Labs., Inc.). Using level-head coordinates, the platinum-iridium lesion electrode (10% iridium, 90% platinum wire, 28 ga.) was lowered vertically to the basolateral amygdaloid region. Coordinates ranged from 2–3.0 mm. behind the bregma, 4.25–5.0 mm. lateral to the midline, and 7.8–8.5 mm. below the dura. Anodal currents passed through the exposed ½-mm. electrode tip with a foot or an ear bar as the indifferent and ranged from 3 ma. for 30 sec. to 5 ma. for 60 sec. The resulting lesions are nonirritative (B. J. Rolls, 1970). At least 1 wk. (usually 2–3 wk.) was allowed for recovery before the first food-preference test was made. Body weight and water intake were measured daily.

Histology and Division of Animals into Groups

At the completion of experimentation, which included the tests described in B. J. Rolls and E. T. Rolls (1973), the animals were deeply anesthetized with ether and perfused intracardially with .9% saline followed by 10% Formalin. In some cases 6 mo. elapsed after the lesions before the perfusion was made. The brains were removed after at least 3 days in Formalin. A number of the brains were embedded in paraffin wax and 15- μ sections were stained with thionin. An alternative method, which proved successful, was to section the fixed brain manually. In either case, an outline of the extent of the lesion was made on drawings of the rat brain seen in the

coronal plane, taken every 1 mm. from König and Klippel's (1963) atlas.

On the basis of the histology the lesioned rats were divided into two groups for the analysis of the data. Thirty-three rats with bilateral lesions in the region of the lateral amygdala and pyriform cortex formed the Am group. Thirteen of these 33 rats with lesions which bilaterally destroyed the basolateral region of the amygdala formed the BL group. Examples of lesions in the BL group of animals are shown in Figure 2. The lesions were in the area in which neurons activated in stimulus-bound eating and drinking are found (E. T. Rolls, 1973). The body weights and growth rates of the lesioned animals in the BL and Am groups were very similar to the controls (for example, in 14 days, immediately post-operatively for the lesioned groups, the Am group gained 37 gm., the BL group 29 gm., and the controls gained 34 gm.). The water intakes of the rats are described in B. J. Rolls and E. T. Rolls (1973). Twenty-seven lesioned rats were not included in these groups. Of these rats, 4 were used in initial experiments; 2 grew abnormally large incisor teeth; 11 had either asymmetrical, or very small, or badly positioned lesions; and 10 lost weight rapidly and died or were killed within 1 wk. of the lesions. These last 10 rats typically showed aphagia and adipisia, and on autopsy many had a sequestration of yellow or black fluid in the gastrointestinal tract. Their lesions were typically large and were centered on the medial amygdaloid region but often included parts of the internal capsule and the lateral hypothalamus (see Figure 2).

EXPERIMENT 1

The purpose of the experiment was to determine the food preferences of the amygdala-lesioned and control rats.

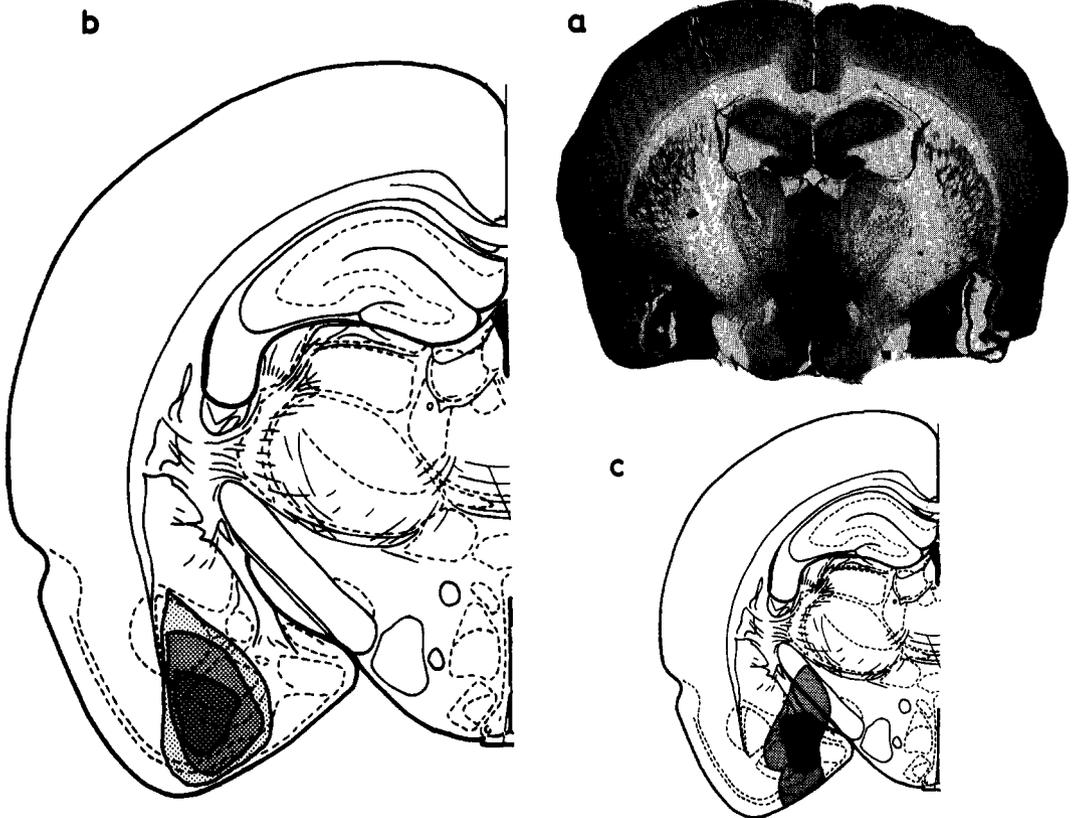


FIG. 2. (a) Examples of lesions typical of the animals with lesions in the basolateral region of the amygdala (BL group). (b) Reconstruction of lesions of the 11 rats in the BL group. (The common region damaged bilaterally in 8, 5, and 3 of the 11 rats is shown by the contours. For example, the overlap region of the lesions in 8 of the rats is shown by the innermost, most densely shaded area. The lesions destroyed a basolateral region of the amygdala. [Outline drawing from König & Klippel, 1963, Plate 37b].) (c) Reconstruction of lesions of 4 of the 10 rats which died after amygdala lesions. (The common region destroyed bilaterally in 3 and 2 of the 4 rats is shown by the contours. The lesions destroyed parts of the central and medial nuclei of the amygdala. [Outline drawing from König & Klippel, 1963, Figure 37b]. In a further three rats the common region was 1.0 mm. further rostral at the same distance from the midline.)

Procedure

In this first food-selection test administered to the rats, the foods were standard chow, cauliflower, orange peel, potatoes, sultanas, and greens (see Figure 1). The chow was identical to that available in the home cages. The other foods were fresh, washed, and uncooked. They were chopped into small portions with the maximum dimension being about .5 cm. The white of the cauliflower was used. The potatoes were peeled. Sultanas are a form of seedless white raisin. The greens were "spring greens," which are green leafy vegetables. Fresh cauliflower leaves and fresh spinach are similar.

Results

In all the food tests, the general behavior of the three groups of animals was similar.

On being placed in the test cage, a rat typically explored the cage for the first 30–90 sec., sniffing and sometimes tasting the foods during this period. Then the rats started to eat the foods, typically eating a particular food for 15 sec.–1 min., then moving on to eat another food. Thus in almost all the tests every food was sampled by the rats. Differences between groups of rats arose because some rats repeatedly returned to a particular food to eat it in preference to the other foods.

The three groups of animals ate for very similar lengths of time (controls for 196 ± 21 sec., Am for 231 ± 16 sec., BL for 245 ± 27 sec.). (The variance figure given through-

out is the SE_M .) These times are not significantly different from each other (i.e., $p > .05$; two-tailed t tests are used throughout this paper).

The Am and BL groups showed very different preferences from the controls. The food preferences of a rat were expressed by converting the time spent on each food to a percentage of the rat's total eating time. In Figure 3 the percentages for each food have been averaged over the different animals in each group. As well as the mean, the standard deviation of the mean percentage of the time a group of rats ate each food was also calculated. A two-tailed t test was used to determine whether a group of rats ate a particular food for a different time to another group of rats. The Am group ate less chow than the controls ($p < .001$), more sultanas ($p < .02$), and more cauliflower

($p < .05$). The BL group ate less chow than the controls ($p < .001$), more sultanas ($p < .01$), and more cauliflower ($p < .01$). Other differences were not significant. The altered food preferences were more extreme in the BL than the Am group (see Figure 3), although a direct comparison of the BL and the Am groups on each of these foods just failed to reach significance ($p > .05$).

Discussion

It can be concluded that the rats with amygdala lesions, particularly in the basolateral region of the amygdala, spent much less time eating standard chow and more time eating sultanas and cauliflower than the controls when placed in the test situation for the first time.

The control group of rats ate little of the unfamiliar foods, consuming chow for 64%

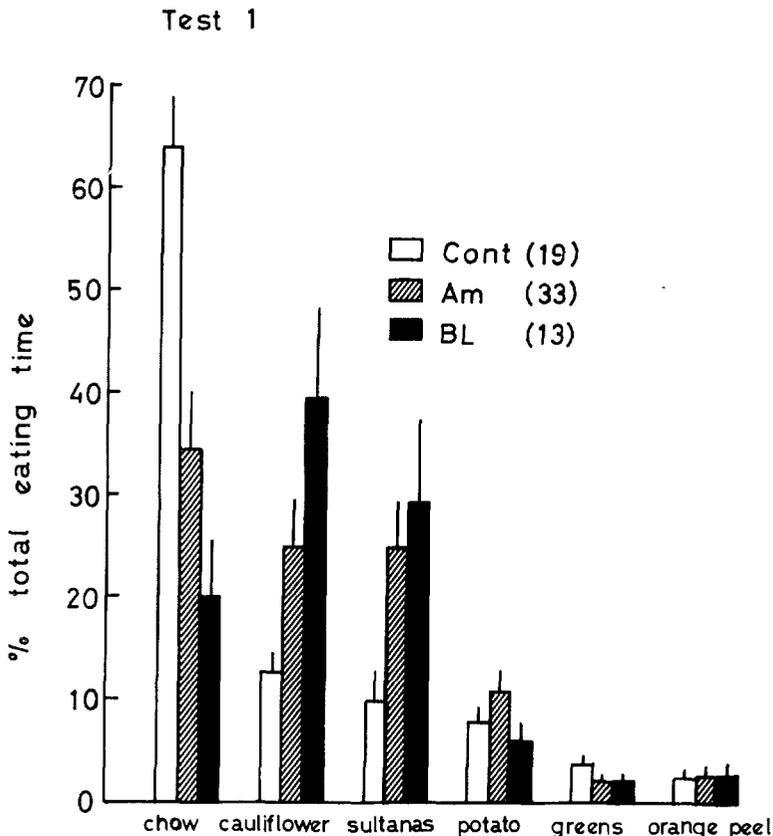


FIG. 3. Food preferences of amygdala-lesioned rats (Am and BL) and control rats. (The BL group had symmetrical lesions in the basolateral region of the amygdala. The number of rats in each group is indicated in parentheses. In this and subsequent figures preferences are indicated by the mean percentage of the total times [histograms $\pm SE$] that the rats ate each food.)

of the eating time. They just sampled the unfamiliar foods. It may be stressed that the chow was familiar because it was normally available in the home cages. The rats with amygdala lesions sampled and ate the new foods, eating chow for only 34% (Am) or 20% (BL) of their eating time.

The control rats may have sampled the unfamiliar foods and found them unpalatable. Therefore, in the rats' second test (Experiment 2) chocolate chip cookies, which are reputed to be highly palatable to rats (Teitelbaum & Epstein, 1962), were included in the foods to determine whether their palatability could coax the controls away from the chow. If this happened, it would be evidence that the altered preferences seen in Experiment 1 after amygdala lesions were a result of altered palatability (e.g., taste, consistency) of different foods.

EXPERIMENT 2

The purpose of the experiment was to determine whether a highly palatable food (chocolate chip cookies) would coax the control rats away from the chow, thus making their food preferences more similar to those of the rats with amygdala lesions.

Procedure

This was the second food selection test administered to the rats. The foods and procedure were the same as for Experiment 1, except that broken chocolate chip cookies (Symbol brand "Maryland Cookies") replaced the orange peel.

Results

The three groups of animals ate for similar lengths of time (controls for 252 ± 16 sec., Am for 298 ± 18 sec., BL for 304 ± 34 sec.). These times do not differ significantly.

The food preferences of the three groups are shown in Figure 4. The Am group ate less chow than the controls ($p < .001$) and more cookies ($p < .01$). The BL group ate less chow ($p < .001$) and more cookies ($p < .001$) than the controls. Other differences were not significant. These altered food preferences were more extreme in the BL than the Am group (see Figure 4). The amount of time that the rats spent eating cookies indicates that the rats found them palatable. For example, the BL group ate them for 58% of their total eating time, and

by the sixth food test (see Figure 6) control rats ate cookies for as much as 32% of their eating time.

Discussion

It can be concluded that the rats with lesions in the amygdala, particularly in the basolateral region, found the cookies very palatable and ate little chow. Although the controls sampled them, the cookies did not coax the controls away from eating primarily chow.

The difference between the amygdala-lesioned rats and the controls may have been that the controls are checked by unfamiliar food; they would not eat significant quantities of an unfamiliar food in unfamiliar surroundings even if it was very palatable. The amygdala-lesioned rats may not have been checked by unfamiliarity. To test this, in Experiment 3 the control rats were retested in the previous two test situations (Experiments 1 and 2) to determine whether with familiarity they would eat proportionately less chow and more of the other foods. It should be recalled that the chow was very familiar to the rats, as it formed their regular diet.

EXPERIMENT 3

The purpose of the experiment was to determine whether with repeated testing the food preferences of the control rats would become like those of the rats with lesions in the amygdala.

Procedure

Further food tests were carried out on 12 of the control rats. In Tests 3 and 4, for which results are not reported here, the rats were offered the same foods as in Experiment 1. Then Tests 5 and 6 were administered to the control rats, forming Experiment 3. Test 5 was a repeat of Experiment 1 (see Figure 1) and Test 6 of Experiment 2. Twelve of the rats, chosen randomly from the unoperated control rats of the preceding experiments, comprised the control group in the present experiments.

Results

In Test 5 the control rats ate for 342 ± 36 sec. compared with 158 ± 17 sec. for the same 12 rats in Test 1 (Experiment 1). The difference is significant ($p < .001$). In Test 6 the control rats ate for 378 ± 27 sec. com-

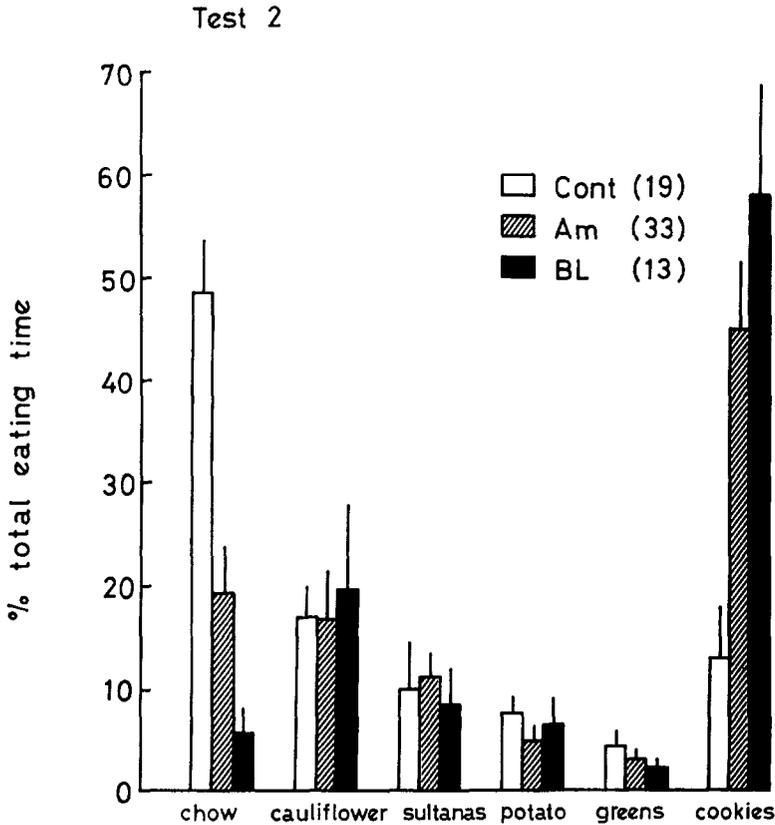


FIG. 4. Food preferences of the amygdala-lesioned (BL and Am groups) and control rats in Test 2, in which cookies replaced the orange peel of Test 1. (See Figure 3 for further details.)

pared with 227 ± 15 sec. for the same 12 rats in Test 2 (Experiment 2). The difference is significant ($p < .001$). Thus, with familiarity, the control rats ate for longer in the test situation. The food preferences of this control group of rats in Test 5 are shown in Figure 5. For comparison, the preferences of these same 12 control rats in Test 1 are shown in Figure 5. It is clear that the rats were eating relatively less chow than in Test 1 ($43.7 \pm 12.2\%$ vs. $58.8 \pm 6.8\%$) and were thus performing more like the Am group in Experiment 1 ($34.4 \pm 5.4\%$). The other main food which the control rats now ate was cauliflower (Figure 5; $41.9 \pm 12.4\%$ vs. $14.2 \pm 2.3\%$ in Test 1).

The food preferences of this control group of rats in Test 6 are shown in Figure 6. For comparison, the preferences of these same 12 control rats in Test 2 are shown in Figure 6. The rats ate less chow than in Experiment 2 ($23.1 \pm 7.7\%$ vs. $44.5 \pm 5.3\%$; $p < .05$)

and were thus performing more like the Am group in Experiment 2 ($19.2 \pm 4.8\%$). The main foods which control rats now ate were cookies ($32.1 \pm 8.4\%$ vs. $12.2 \pm 4.8\%$ in Experiment 2), and cauliflower ($30.1 \pm 7.7\%$ vs. $16.7 \pm 4.3\%$ in Experiment 2; Figure 6).

Discussion

In the repeated tests (5 and 6), when both the testing situation and the available foods were familiar to the rats, the control rats showed food preferences which were similar to those of the rats with amygdala lesions when they were first tested. Thus, the effect of amygdala lesions in this testing situation was to allow the animals to eat unfamiliar palatable foods in an unfamiliar situation. The purpose of Experiments 4 and 5 was to determine whether the intact rats were reacting to unfamiliarity of the foods or unfamiliarity of the testing situation.

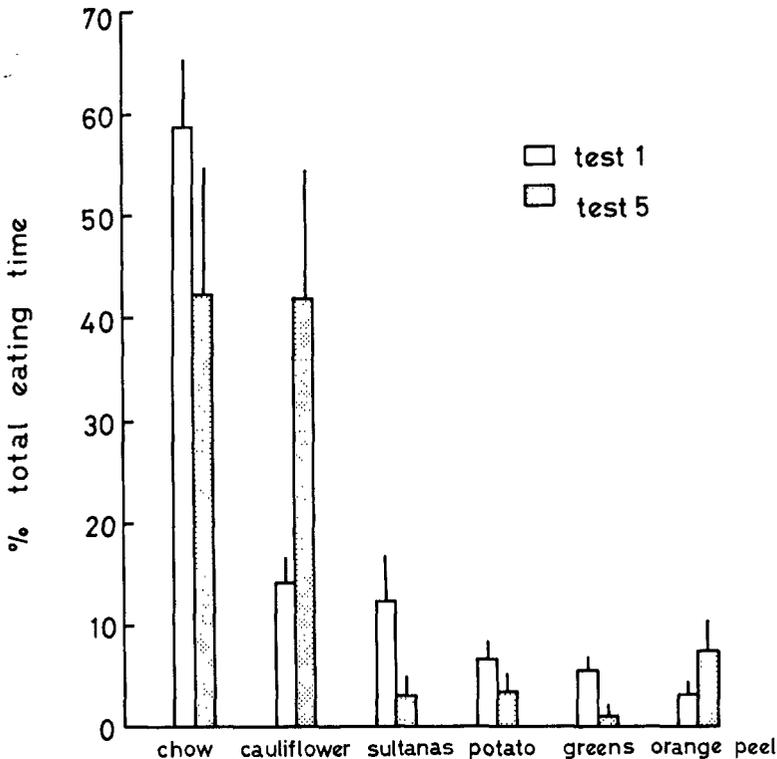


FIG. 5. Food preferences of 12 control rats in Test 5, in which the foods were the same as those available in Test 1. (For comparison, the food preferences of the same 12 control rats in Test 1 are shown in the unshaded histogram. See Figure 3 for further details.)

EXPERIMENT 4

A number of new foods were given to the animals in the familiar testing situation. The purpose of the experiment was to determine whether unfamiliar foods would be sufficient to make intact control rats again eat a large proportion of their familiar chow compared to the amygdala-lesioned rats.

Procedure

The test cage and procedure were as described for the earlier tests. The foods were standard chow and sultanas and the following unfamiliar foods, arranged as shown in the inset to Figure 7: tomato, banana, mushroom, and carrot. These new foods were fresh, uncooked, and chopped into small portions with a maximum dimension of .5 cm. There were 12 of the original 19 controls remaining in the control group, and 11 animals in the amygdala-lesioned group. Six of the 11 amygdala-lesioned animals were from the BL group. All the rats had been tested at least four times in the test cage, so that the test cage and procedure were familiar to the animals.

Results

The amygdala-lesioned and control groups of animals ate for similar lengths of time (247 ± 26 sec. and 288 ± 20 sec., respectively). These times are not significantly different.

The food preferences of the groups are shown in Figure 7. The amygdala-lesioned animals ate much less chow than the controls ($16.7 \pm 3.4\%$ and $45.7 \pm 8.3\%$, respectively; $p < .01$). Thus, an unfamiliar selection of foods was sufficient to make the control rats spend a greater percentage of time eating chow than the lesioned rats. The amygdala-lesioned animals sampled and ate the new foods, and ate significantly more mushrooms than the controls ($28.1 \pm 5.3\%$ and $8.0 \pm 4.0\%$, respectively; $p < .01$).

Discussion

It can be concluded that intact rats sample unfamiliar foods, but eat only a small

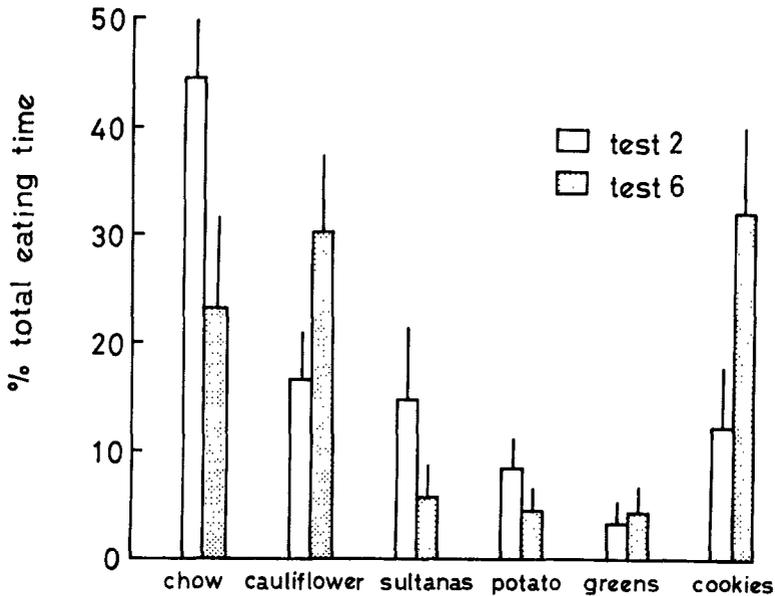


FIG. 6. Food preferences of 12 control rats in Test 6, in which the foods were the same as those available in Test 2. (For comparison, the food preferences of the same 12 control rats in Test 2 are shown in the unshaded histogram. See Figure 3 for further details.)

amount on first exposure, while rats with amygdala lesions both sample new foods and eat them immediately if they are palatable. Presenting the control rats with a selection of unfamiliar foods was sufficient to make them eat their familiar chow for a high proportion (45.7%) of the time, relative to the lesioned animals. The familiarity or unfamiliarity of the situation in which the food was found did not appear to be important in determining whether the rats would eat familiar rather than unfamiliar foods (see General Discussion section).

EXPERIMENT 5

The purpose of this experiment was to determine whether unfamiliarity with the test situation, which could lead to fear, is a significant factor in making intact animals eat familiar chow rather than relatively unfamiliar foods. If fear due to the test situation were a significant factor this could be a way in which the amygdala-lesioned rats differed from the controls. It has been shown already in Experiments 1-4 that the major factor in determining the preferences of the intact animals is familiarity/novelty of palatable foods and that the amygdala-lesioned animals will eat novel foods.

Procedure

Experiment 1 was repeated on control and lesioned rats twice more, with and without disturbing environmental stimuli to make the test situation unfamiliar and to induce fear. The normal and noxious environmental conditions were run in a counterbalanced experimental design, with at least 2 days between tests for each animal. The environment was made disturbing by playing a tape recording of loud irregular sounds throughout each 10-min. test and by concurrently making sudden movements which the rat could see in the well-lit test room. The standard tape recording had been made by banging the microphone during the recording. The sudden distracting movements were made by the experimenter's arms, which did not come closer than 1 m. to the test cage. The subjects were 10 of the amygdala-lesioned rats and five of the controls, run blindly by the experimenter.

Results

Although the disturbances reduced the total eating times of control (192 ± 37 sec. vs. 254 ± 39 sec.) and amygdala-lesioned rats (213 ± 27 sec. vs. 237 ± 26 sec.), these differences were not significant. The disturbances also delayed the times to the onset of eating. These were 151 ± 62 sec. vs. 84 ± 27 sec. for the controls and 158 ± 29 sec. vs. 89 ± 11 sec. for the amygdala-lesioned rats. This effect of the disturbances on the le-

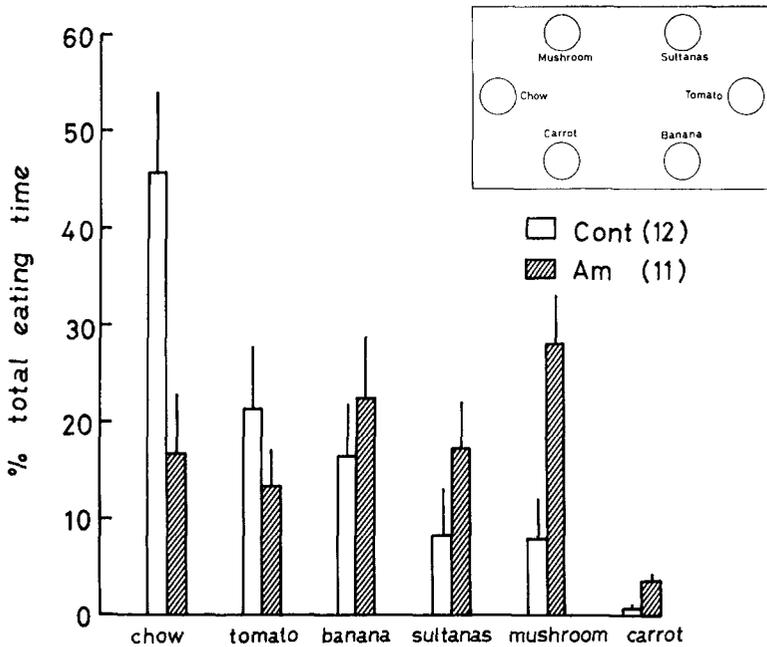


Fig. 7. Food preferences of amygdala-lesioned (Am) and control rats in Experiment 4, in which four new foods (tomato, banana, mushroom, and carrot) were introduced. (The inset shows the arrangement of the foods. See Figure 3 for further details.)

sioned group was significant ($p < .05$). It is thus clear that the presence of the noise and movements did affect the animals' behavior.

The food preferences of the four groups are shown in Figure 8. It is clear that the presence of the disturbances had no significant effects on the food preferences of the animals.

Discussion

It is concluded that fear induced by an unfamiliar and disturbing environment was not sufficient in the test situation to alter the rats' preference for foods.

Additional evidence is provided in Figure 8 about the effects of unfamiliarity/novelty of the foods. All the rats had been given tests with foods similar to these previously (see previous experiments). With this high degree of familiarity, the preferences of the control rats had become very similar to those of the rats with amygdala lesions, the main remaining differences being in chow and sultanas.

GENERAL DISCUSSION

In this study rats with lesions in the amygdala did not have major defects in the

control of the amount of food they ate. For example, their body weights increased as rapidly as those of the intact rats. Further, in the 10-min. food-selection tests used in these experiments, there were never any significant differences in the amounts of time the control and lesioned groups ate in any one test. This finding is in agreement with that of other workers, who have failed to find that amygdala lesions in rats alter body weight regulation in a way comparable with the changes following hypothalamic damage (Grossman & Grossman, 1963). In dogs, changes in body weight regulation follow amygdala lesions, but these changes also are not as large as those which follow hypothalamic damage (Fonberg, 1969). It is of interest that in the dog, the critical region of the amygdala which when lesioned leads to aphagia and then hypophagia is localized in the region of the central and medial nuclei (Fonberg, 1969, p. 347). This corresponds closely with the area in which a lesion leads to aphagia in the rat (see Figure 2).

By testing for food preferences, a major change in the ingestive behavior of the amygdala-lesioned rats was found (Experi-

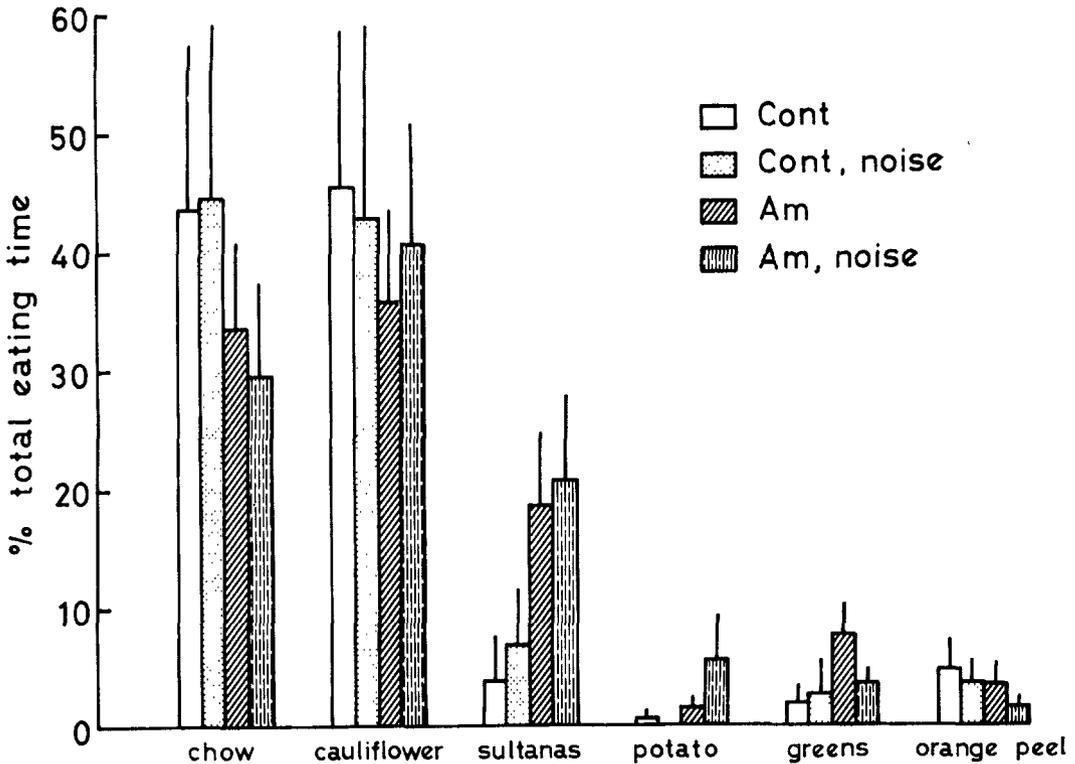


FIG. 8. Food preferences of 10 amygdala-lesioned (Am) and 5 control rats in Experiment 5, in which noises and movements (noise) were introduced in one of two preference tests received by each rat. (See Figure 3 for further details.)

ments 1 and 2). The lesioned rats sampled and ate new palatable foods, in contrast to the intact rats, which sampled the new foods but ate mainly the standard chow which formed their normal diet. The reason that the control rats preferred chow was not that they found the new foods unpalatable. After repeated testing had familiarized the controls with the new foods, they switched to preferring some of the new foods. Their preferences thus became similar to the amygdala-lesioned rats' preferences (Experiment 3 and also 5). Lack of familiarity with the new foods, rather than with the testing situation, is the important factor; when unfamiliar foods were introduced into the familiar testing situation, the control rats ate much more chow than the amygdala-lesioned rats, which ate the palatable new foods (Experiment 4). This conclusion is supported by the finding that altering the testing situation was not sufficient to alter the food preferences of the rats (Experiment

5). Further, any general factor such as fear in the testing situation was not important enough to cause differences in the eating times among the groups of animals in any one experiment. It is concluded that the amygdala-lesioned rats do not have the normal control which prevents rats' eating large quantities of new palatable foods. It appears that in this way the amygdala is involved in the selection of foods eaten.

The rats with amygdala lesions did not eat foods indiscriminately. In every experiment it was found that the lesioned rats showed marked differences in the time spent eating the different foods. These time differences probably represent preferences and aversions, because all the foods were sampled. Thus, a change in reward value in terms of the palatability of the different foods was not a major alteration produced by the lesions; rather, the reward value computed with the aid of previous experience appears to be the aspect of ingestive

behavior altered by the lesions. This previous experience could be of many different types—for example, that which is involved in “neophobia” (Barnett, 1958; Galef, 1970; Richter, 1953; Rozin, 1968; Shorten, 1954; Weiskrantz & Cowey, 1963) or in learned aversion (Galef & Clark, 1971; Garcia & Koelling, 1967; Nachman, 1963). Learned aversion was certainly impaired in these amygdala-lesioned rats (see following article).

The basolateral region of the amygdala appears to be important in the altered food selection. In Experiments 1 and 2, the BL group (13 rats with bilateral lesions in the basolateral region of the amygdala) showed the altered food preferences more markedly than the Am group (i.e., rats with bilateral lesions in the lateral amygdala/pyriform cortex region; this group included the BL rats). This finding provides strong corroborative evidence for the suggestion that the basolateral region of the amygdala is involved in ingestive behavior (E. T. Rolls, 1972, 1973). This suggestion was based on the following series of experiments. First, neurons in the basolateral amygdala are activated in eating elicited by electrical stimulation of the lateral hypothalamus (E. T. Rolls, 1972). Second, these neurons have absolute refractory periods similar to those involved in the stimulus-bound eating (E. T. Rolls, 1973). Third, the injection of a local anesthetic bilaterally into the amygdala blocks stimulus-bound eating (P. H. Kelly, manuscript in preparation).

These results taken together suggest that stimulus-bound eating may arise when amygdaloid neurons normally involved in the control of ingestive behavior are activated, simultaneous activation of brainstem neurons also being important (see B. J. Rolls & E. T. Rolls, 1973; E. T. Rolls, 1972). The amygdaloid neurons may normally be involved in the selection of ingested foods on the basis of previous experience (Experiments 1-5) and therefore when foods are rewarding. Excitation of these neurons in stimulus-bound eating may therefore make food in the cage rewarding and lead to eating. This may explain some peculiar characteristics of stimulus-bound eating (Val-

enstein, Cox, & Kakolewski, 1970)—for example, the degree of specificity of the different substances which may be ingested in stimulus-bound motivational behavior.

Altered feeding behavior has previously been found to follow lesions or stimulation of the amygdala in the rat. Electrical stimulation of the “cortico-medial-pyriform transition zone” of the amygdala suppressed food intake in deprived rats (White & Fisher, 1969). Lesions of the corticomедial amygdala increased the latency to the onset of eating in a novel environment (Sclafani, Belluzzi, & Grossman, 1970). As the cortico-medial region of the amygdala was involved in the experiments, the results can not be directly compared with the present findings. In experiments on the ventral amygdala, it has been found that in deprived rats adrenergic stimulation of the ventral amygdala produces an increase in food intake and a decrease in water intake. In deprived rats, cholinergic stimulation of the same site increased water intake and reduced food intake (S. P. Grossman, 1964). The aim of the present experiments was to examine changes in ingestive behavior following destruction of the basolateral region of the amygdala, the region found to be activated in stimulus-bound eating and drinking (E. T. Rolls, 1972).

Altered food preferences follow lesions of the amygdala in monkeys. Following the lesions, the monkeys will accept meat (Ursin, Rosvold, & Vest, 1969) and will accept strong saccharine solutions (Weiskrantz, 1960). Monkeys after bilateral temporal lobectomy, which involved the amygdala but also many other structures, showed repeated oral investigation of inedible objects (Klüver & Bucy, 1939). The extent to which these changes are dependent on altered control of ingestive behavior by previous experience, as appears to be the case in the rat, is unknown.

The altered ingestive behavior of the amygdala-lesioned rats was brought out well in the 10-min. food-preference experiments described. The test situation was also effective in showing that the effects of amygdala lesions were not due to interruption of

the olfactory pathways, for olfactomized rats in the same situation showed very different behavior (E. T. Rolls & M. Burton, unpublished results, 1971). The olfactomized rats ate for very much shorter times than control rats but had food preferences which were similar to the control rats.

The present finding that the amygdala influences food intake suggests that functional connections exist between the amygdala and the diencephalic systems which control feeding. This suggestion is consistent with the discussion above on the function of the amygdalo-hypothalamic connections. The role of the amygdala in ingestive behavior in general is discussed at the end of the following paper.

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