INSTRUMENTAL REACTIONS AND FOOD AND WATER INTAKE IN MEDIAL AMYGDALA RATS

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Abstract. Rats were trained preoperatively to perform instrumental reactions for food and water reward on a continuous reinforcement schedule. Two levers on two opposite sides of the Skinner box were available. Each press of the first lever delivered one drop of water and each press of the second lever — one pellet of solid food. After the electrolytic lesions of the medial part of the amygdaloid complex, rats were hypophagic and hypodipsic. Most of the animals showed, however, only small decreases of total unconditioned daily water and food intake. On the other hand, the instrumental performance was markedly impaired, in particular for water reinforcement. Histological verification showed that lesions were restricted to the amygdaloid complex and involved mainly the ventral part of medial nucleus.

INTRODUCTION

Previous results obtained on dogs (7–10, 14) showed that dorsomedial amygdala lesions produced aphagia and impairment of the instrumental performance, while the results obtained by the other authors on the rats were controversial. Total aphagia and adipsia after bilateral amygdala lesions involving mostly its medial portion in the rats were observed by several authors (4, 18–20, 37, 38, 43, 50). Also Koikegami (20) obtained hypophagia and decrease in appetite after destruction of basal and medial nuclei. On the other hand Anand and Brobeck (2), and Pubols (34) did not obtain changes in alimentary behavior after amygdala lesions and Sclafani et al. (39) have found only the prolonged latency to initiation of eating in novel environment.
The dimensions and localizations of the amygdala lesions in rats varied in the experiments of respective authors and this might be the cause of the controversial results. Therefore it seemed important to examine the effects of amygdala lesions comparable to those which produced obvious alimentary disturbances in our previous experiments on dogs.

Grossman and Grossman (17) have found reduction of the water intake without changes in the food intake, in rats with medial amygdala lesions, therefore it was worthwhile to study also these relations. In addition, we were also interested in the motivational aspects of the amygdala damage using the instrumental performance as an indicator of the motivational level.

MATERIAL AND METHODS

Experiments were performed on 20 naive, hooded rats, 3–4 mo. old, weighing 250–350 g at the start of the experiments. The animals were randomly divided into four groups each of five rats in two experiments:

Experiment I. Experiment I involved unconditioned group (UAM) with lesions in medial part of the amygdala and unconditioned control group (UC) with sham operation. In both groups the experimental procedure was the same: daily food and water intake and body weight in individual home cages were registered 15 days before operation and 15 days after operation. Food consisted of standard purina chow available ad lib. in food bowls. Pure water was present in standard hanging bottles.

Experiment II. Experiment II involved instrumental group (IAM) with operation in medial part of the amygdala and instrumental control group (IC) with sham operation.

The animals of both control and operated groups were trained preoperatively to perform instrumental responses for food and water reward under continuous reinforcement schedule 1:1. The apparatus was an experimental box 30 cm × 30 cm wide, containing two levers situated on the opposite sides. The levers were 4 cm wide aluminum bars, inserted 2.4 cm distant from the wall of the box and 4 cm over the floor. Both feeders for food and water were situated 1 cm on the right side of each lever on the same level above the floor. Each press of one lever delivered one drop of water and each press of the second lever — one standard pellet of solid food. The resistance of both levers was balanced and in both cases the effective force pressing had to be more than 10 g.
Experimental session lasted 30 min. After termination of each experimental session the rats were placed in their individual home cages, where they received 1 h later 10 g of the standard purina chow solid food and 10 ml of water. Thereafter the food and water were not available. The rats were tested in the instrumental situation for 4 wk. During this time each 5 days of training was followed by an interval of balanced nutrition. In the first 24 h of the interval, food and water were available ad lib. and in the next 24 h the animals were returned to the previous conditions of deprivation. During first 2 wk of preoperative training the rats were adapted to the experimental procedure. During this time they attained the criterional level of performance, i.e., an average of 100 lever-presses per session for food-pellets and about 200 lever-presses per session for water, computed respectively from five, consecutive days. Only the instrumental performances observed in last 2 wk before surgery were taken into account for further analysis and comparison with postoperative level. After 5 days of recovery from surgery, the animals were retested using the same procedure, i.e., the instrumental performance was observed from 6–10 and from 12–16 days after operation.

Surgery. Bilateral lesions were made under Nembutal anesthesia (50 mg/kg) by passing an anodal direct current of 2.5 mA per 15 s through the unipolar wolfram electrode of 0.1 mm in diameter, insulated by enamel except for 0.2 mm on the tip. The circuit was completed by means of a rectal cathode. Coordinates, according to the König and Klippel (21) atlas were: AP + 5.7, H – 2.7, L + 3.2.

The sham operation was performed by introduction into the brain of the same kind of electrode, at the same stereotaxic coordinates, but without passing the electrical current.

Histology. When the experiment was completed, rats were sacrificed by overdose of ether, their brains were removed and preserved in 10% formaline. Then, frozen sections in frontal plane of 15 μm wide were cut. Each fifth section was stained by the Klüver or by the Nissl methods alternatively, mounted on slides and examined for the localization and the extent of the lesions. The lesions were reconstructed by drawing made directly from the microscopic slides projected on a screen.

Statistics. Data obtained from both experiments were elaborated by the analysis of variance (mixed design, type I (25)). All experimental sessions were divided into blocks of five consecutive sessions. In this way six blocks were obtained for UC and six blocks for UAM groups (3 before and 3 after operation) and four blocks were obtained for IC
and IAM groups (2 before and 2 after operation). The sums from these blocks were analyzed, respectively for individually measured parameters. In the second stage Duncan test (35) was applied to data obtained from the analysis of variance.

RESULTS

Experiment I. Figure 1 presents unconditioned food and water intake before and after operation in UAM group. Each bar represents mean value from 5 days of observations for the individual subjects. It may be seen that rats with medial amygdala lesions reduced their water and food intake. The decrease of water intake lasted for 3 to 7 days after operation. Food intake was also reduced but for a shorter period of time (1–4 days). The mean postoperative amount of water and food intake varied in individual subjects from 20% to 75% of the preoperative level.

Fig. 1. Unconditioned daily water and food intake for individual rats in unconditioned group (UAM). Each bar represents mean value from 5 days of observation for the individual subjects. First bar (striped), last 5 days period before operation; two next bars (white), 1–5 and 6–10 days after operation.
TABLE I

Analysis of variance (mixed design type I — Lindquist, 1953) of the amount of unconditioned water and food intake and body weight in UAM and UC groups (for the time of all six block of experimental days)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Water intake</th>
<th>Food intake</th>
<th>Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>MS</td>
</tr>
<tr>
<td>Control/operated group</td>
<td>1</td>
<td>2,801.667</td>
<td>6.288*</td>
<td>2,331.267</td>
</tr>
<tr>
<td>error (b)</td>
<td>8</td>
<td>444.533</td>
<td>—</td>
<td>510.558</td>
</tr>
<tr>
<td>Blocks of time</td>
<td>5</td>
<td>1,342.587</td>
<td>16.746***</td>
<td>631.147</td>
</tr>
<tr>
<td>Interaction</td>
<td>5</td>
<td>517.227</td>
<td>6.451***</td>
<td>120.267</td>
</tr>
<tr>
<td>error (w)</td>
<td>40</td>
<td>80.173</td>
<td>—</td>
<td>75.098</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Interactions</th>
<th>df</th>
<th>MS</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interaction</td>
<td>5</td>
<td>120.267</td>
<td>1.601</td>
</tr>
<tr>
<td>Interaction</td>
<td>40</td>
<td>848.125</td>
<td>—</td>
</tr>
</tbody>
</table>

* P < 0.05; *** P < 0.001.

Fig. 2. Mean values of body weight of rats of unconditioned group (UAM) before and after operation. Each bar represents mean body weight measured during 5 consecutive days. Stripped bars, operated group; open bars, control group.

The analysis of variance, mixed design type I (25) was used twice. Once, to compare all the operated and control groups (see Table I) through the whole period of experiment and, additionally, to compare two periods: preoperative and postoperative (Table II). Means for groups, where the differences were statistically significant, were elaborated using the Duncan test (35). It was found that values of both unconditioned water and food intake in first blocks of first 5 days after operation were significantly different (P < 0.01) from preoperative values. In the second block of next 5 days after operation the level did not differ statistically.
Analysis of variance (mixed design type I — Lindquist 1953) of the amount of unconditioned water and food intake and body weight in UAM and UC groups (for the separated blocks of time before and after operation)

| Source of variation | df | Water intake before | | Water intake after | | Food intake before | | Food intake after | | Weight before | | Weight after |
|---------------------|----|---------------------|--|---------------------|--|---------------------|--|---------------------|--|---------------------|--|---------------------|--|
|                     |    | MS                  | F | MS                  | F | MS                  | F | MS                  | F | MS                  | F | MS                  | F |
| Control/operated    | 1  | 282.133             | 1.434 | 3,370.800          | 9.700* | 644.033             | 1.645 | 1,840.833          | 8.121* | 86.325             | < 1 | 30,720.000          | < 1 |
| group error (b)     | 8  | 196.633             | —   | 347.483             | —   | 391.333             | —   | 226.650             | —   | 43,162.500          | —   | 52,222.916          | —   |
| Blocks of time      | 2  | 241.467             | 6.635** | 2,452.033          | 21.376*** | 19.633             | < 1 | 1,344.900          | 15.085*** | 31,975.833          | 163.454*** | 18,350.833          | 42.946 |
| Interaction error (w)| 2  | 24.133              | < 1 | 843.300             | 7.351** | 71.633              | 1.595 | 152.233             | 1.707 | 2,700.833           | 13.806*** | 322.500             | < 1   |
|                     | 16 | 36.433              | —   | 114.708             | —   | 44.883              | —   | 89.150              | —   | 195.625             | —   | 427.291             | —   |

* P < 0.05; ** P < 0.01; *** P < 0.001.
(P < 0.05) from the preoperative level. The Duncan test for correlated data have shown the differences in first postoperative block for water (P < 0.05) and for food (P < 0.01).

Changes in the body weight of UAM and UC groups are presented in Fig. 2. It is seen that both in UAM and UC groups the body weight was slightly reduced in the first 5 days after operation. Analysis of variance did not reveal statistically significant influence of the amygdala lesions on the body weight in operated animals (Tables I and II). However, the analysis of correlation showed the correlation of the body weight with time both before and after operation in all rats from operated and control groups (P < 0.05).

**Experiment II.** The changes of instrumental performance reinforced by water or food, before and after amygdala lesions, are presented in

![Graph](image)

Fig. 3. Instrumental performance in 30 min tests for individual rats in instrumental group (IAM). First bar (stripped), last 5 days period before operation; two next bars (white), 6-10 and 12-16 days after operation.
Fig. 4 Cumulative values of mean instrumental performance for instrumental group (IAM) (upper) and control group (IC) (lower) in consecutive experimental sessions. A, B: before operation; C, D: after operation. Circles, bar-pressing for water; rectangles, bar-pressing for pellets.

**Table III**

Analysis of variance of the level of the instrumental performance in IAM and IC groups (for all four blocks of experimental days)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Water instrum. perform.</th>
<th>Food instrum. perform.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Control operated group</td>
<td>1</td>
<td>3,485,721.600</td>
<td>11.636**</td>
</tr>
<tr>
<td>error (b)</td>
<td>8</td>
<td>239,555.225</td>
<td>—</td>
</tr>
<tr>
<td>Block of time</td>
<td>3</td>
<td>2,507,844.600</td>
<td>49.299**</td>
</tr>
<tr>
<td>Interaction</td>
<td>3</td>
<td>1,767,061.261</td>
<td>34.737***</td>
</tr>
<tr>
<td>error (w)</td>
<td>24</td>
<td>50,869.141</td>
<td>—</td>
</tr>
</tbody>
</table>

**P < 0.01; ***P < 0.001.
**Table IV**

Analysis of variance of the level of the instrumental performance in IAM and IC groups (for the separates blocks of experimental days before and after operation)

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Water instrumental performance before</th>
<th>F</th>
<th>MS</th>
<th>Food instrumental performance before</th>
<th>F</th>
<th>MS</th>
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</thead>
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<td></td>
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<td></td>
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<tr>
<td>Control/operated group</td>
<td>1</td>
<td>88,844.450</td>
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<td></td>
<td>8,634,294.050</td>
<td>53.374***</td>
<td>32,562.450</td>
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<tr>
<td>error (b)</td>
<td>8</td>
<td>240,530.950</td>
<td></td>
<td>1,294,138.400</td>
<td></td>
<td>8,810.350</td>
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</tr>
<tr>
<td>Blocks of time</td>
<td>1</td>
<td>684.450</td>
<td>&lt;1</td>
<td></td>
<td>207,468.450</td>
<td>7.482*</td>
<td>994.050</td>
</tr>
<tr>
<td>Interaction</td>
<td>1</td>
<td>54,392.450</td>
<td>2.457</td>
<td>9374.450</td>
<td>&lt;1</td>
<td>13,261.250</td>
<td>2.452</td>
</tr>
<tr>
<td>error (w)</td>
<td>8</td>
<td>22,135.450</td>
<td></td>
<td>221,831.600</td>
<td></td>
<td>5,407.900</td>
<td></td>
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</table>

* \( P < 0.05; \)** \( P < 0.01; \)** \( P < 0.001. \)
Figs. 3 and 4. In Fig. 3 it is shown that the instrumental performance for water is evidently reduced during two consecutive postoperative blocks of five sessions in all individual subjects. The instrumental performance for solid food is reduced mainly in the first block and thereafter returns almost to the preoperative level. It should be noted that the first block of instrumental postoperative training coincided in time with the

Fig. 5A. Reconstruction of the lesions on the sections through areas of maximum tissue destructions in individual brains of animals for unconditioned (UAM) group.
second postoperative block of unconditioned group (see Fig. 1), i.e., when the unconditioned food and water intake had been fully recovered in all rats but one. Figure 4 shows the cumulative curves of the mean number of instrumental reactions performed in the two blocks of 5 days of consecutive experimental sessions for lesioned IAM and control IC groups. The curves represent the mean number of reactions for the

Fig. 5B. Reconstruction of the lesions for instrumental (IAM) group.
whole group during five consecutive days. Each first point of the curve represents mean value from first experimental sessions for the whole group. Each next point is the sum of the mean values of the previous consecutive session plus the mean values of the session corresponding to this point. It is seen that only the instrumental performance reinforced by water was dramatically reduced. The instrumental performance reinforced by solid food also decreased postoperatively but to a lesser extent.

**Table V**

Comparison of localization of lesions in particular nuclei of the amygdala in individual rats. AMe, medial n.; ACr, cortical n.; ABm, basomedial n.; ABI, basolateral n.; ACE, central n.; m. intercal.; massa intercalata. A, UAM group; B, IAM group.

<table>
<thead>
<tr>
<th>Rat's number</th>
<th>AMe n.</th>
<th>A Cr n.</th>
<th>ABm n.</th>
<th>ACE n.</th>
<th>AL n.</th>
</tr>
</thead>
<tbody>
<tr>
<td>101</td>
<td>L</td>
<td>D</td>
<td>V</td>
<td>M</td>
<td>V</td>
</tr>
<tr>
<td>177</td>
<td>L</td>
<td>R</td>
<td>V</td>
<td>M</td>
<td>L</td>
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<tr>
<td>188</td>
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<td>R</td>
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<td>L</td>
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<tr>
<td>189</td>
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<td>R</td>
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<td>L</td>
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<tr>
<td>200</td>
<td>L</td>
<td>R</td>
<td>V</td>
<td>M</td>
<td>L</td>
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</tbody>
</table>

A

<table>
<thead>
<tr>
<th>Rat's number</th>
<th>AMe n.</th>
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<th>ABm n.</th>
<th>ACE n.</th>
<th>AL n.</th>
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<tr>
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<td>V</td>
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</tr>
<tr>
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<td>R</td>
<td>V</td>
<td>M</td>
<td>L</td>
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<td>151</td>
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<td>L</td>
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<td>153</td>
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<td>L</td>
<td>R</td>
<td>V</td>
<td>M</td>
<td>L</td>
</tr>
</tbody>
</table>

**B**

The analysis of variance (Tables III and IV) shows a significant reduction of the values of the instrumental performance reinforced both by water and food after operation. The Duncan test revealed statistically significant differences for two postoperative mean differences on the
level \( P < 0.01 \) from preoperative and postoperative control values. In the case of food reinforced instrumental performance the Duncan test has shown statistically significant differences (on the level \( P < 0.01 \) for value of first block of postoperative experimental period of time and on the level \( P < 0.05 \) for the values of the second one.

The results of histological verifications of UAM group are shown in Fig. 5A and Table VA. In all subjects of this group the lesions were localized bilaterally in medial nucleus of the amygdala, not involving the whole nucleus, but also not exceeding the amygdaloid complex. As we see from Table VA small parts adjacent to the medial nucleus of the basal, cortical and central nuclei were involved in some cases whereas the lateral nucleus was never touched. The results of histological verifications of IAM group are shown in Fig. 5B and Table VB. In all cases lesions involved the medial part of the amygdala bilaterally. It is seen in Table VB that in all subjects the medial nucleus in rostral or intermediate part in anteroposterior plan is bilaterally destroyed and involved only in a few cases small portions of the basal, cortical and central nuclei. The lesions in both groups do not exceed the level of optic tract in dorsoventral dimension. A comparison of lesions of the UAM and IAM groups shows very great similarities in respect to localizations and dimensions.

**DISCUSSION**

The results of our experiments clearly show that small bilateral lesions of the medial part of the amygdaloid complex in rats produce changes in alimentary behavior. These results have several interesting implications. Firstly it was demonstrated that the impairment of the instrumental performance reinforced by water and food was deeper and more persistent than impairment of the unconditioned daily water and food intake in the home cage. Secondly, we found that under the conditions of free choice of two kinds of reinforcement the decrease of instrumental performance reinforced by water was more prominent than that reinforced by solid food.

It should be taken into account that alimentary disturbances observed in our experiment lasted a shorter time and were less prominent than those described earlier in rats by other authors. Some authors (4, 18, 19, 37) observed aphagia and adipsia eventually leading to extreme inanition or even death following amygdala lesions in rats. We have never observed such dramatic changes in rats after small lesions restricted to medial amygdalar area. We did however observe such disturbances after lesions involving larger area extending dorsally beyond the amygdala (Korczyński and Fonberg, in preparation). It is possible, that similar
damage may account for such dramatic changes in alimentary behavior observed by the above authors. The possibility of the impairment of pallido-fugal system (28) and/or nigrostriatal bundle (47) should be taken into account. In our present experiments lesions were strictly localized in medial part of the amygdala and did not exceed the level of the optic tract in any case.

On the other hand, Fonberg (7-10, 12) observed in dogs aphagia and adipsia after dorsomedial amygdala lesions, also in the cases when lesions were limited to the amygdala. It should be stressed that the effects of amygdalar lesions in dogs, were much more pronounced concerning both food intake and instrumental performance than those in rats. One possible explanation of this is that the amygdala plays a different role in the regulation of alimentary behavior in various species. This conclusion might be supported by anatomical findings. Powell et al. (33) and Leonard (23a) did not report direct projections from the neocortex to the amygdala in rats. Neither were there found any direct projections from the rat's amygdala to the neocortex (5, 6, 24). However in dogs (22), monkeys (29) and cats (48) such direct connections were described.

It is also likely, that the differences between the effect of the dorsomedial amygdala lesions in dogs and rats are due to a greater encephalization in dogs than in rats. On the basis of previous experiments on dogs we may conclude that the amygdala is in this species involved in social and emotional behavior related with humans which may depend on cortical connections (11, 12). In this respect getting of food is much more closely related with social and emotional behavior in dogs than in rats. The amygdala lesions by impairing in dogs the emotional components of the alimentary act may have more dramatic effects than in rats. Another explanation of the differences between the results in dogs and in rats is that the amygdalar lesions in our rats did not involve the whole medial nucleus, which in this species is comparatively bigger than in dogs. In rats the damage was limited to a smaller part of the dorsomedial amygdala, as compared to lesions in dogs and, therefore, it might be localized in the area which was not crucial for the alimentary mechanisms.

Coming back to the question of why the instrumental responses in rats were more impaired than free consumption of water and food it seems justified to hypothesize that unconditioned alimentary behavior in the rats is more dependent on hypothalamic than on amygdalar mechanisms and therefore the compensation by hypothalamus in these animals takes place earlier than in dogs. Thus, in rats medial amygdala lesions impair mainly the instrumental responses, because the unconditioned component of alimentary act is compensated by hypothalamus.
The additional factor which should be taken into account in analyzing the impairment of instrumental performance might be the decrease of the general activity after amygdala lesions. This may explain why the unconditioned feeding and drinking, which needs less effort than instrumental bar pressing is less disturbed. In our experiments in dogs the instrumental procedure was different than in rats. The dog press the bar once in response to each conditioned signal, with 1–3 min intervals between signals and therefore during one experimental session the maximal number of correct presses is up to 20. In this case the fatigue does not play an essential role, whereas in the rat, in which in a continuous bar pressing schedule it presses as much as 200 times per session or even more the decrease of the general activity and/or greater fatigue than before operation may produce the decrement of bar pressing. Also the relatively greater decrease of bar-pressing for water after the operation might be produced by the fact that preoperatively the rats perform much more presses per sessions for water than for food reinforcement which, therefore, need much more effort to reach the preoperative level of water-reinforced than of food-reinforced performance. The experiments on the effect of amygdala lesions of the general activity of the rats, which are now in progress will elucidate this point.

The next problem is concerned with the neuronal organization of the control mechanisms of drinking and feeding behavior. Grossman and Grossman (17) reported that in rats after medial amygdala lesions water intake was reduced without changes in food intake. However, our experiments showed that the rats with medial amygdala lesions were not only impaired in water intake but the food intake was also reduced, though this last decrease was less evident. Similar results were obtained on the rats (4, 43, 50) and on the dogs (13). In all these investigations amygdala lesions produced both aphagia and adipsia but adipsia always outlasted aphagia. Thus, it is probable, that medial amygdala of rats is mostly involved in the regulation of water intake, although these mechanisms may overlap with the mechanisms of food regulation. A partial support for this hypothesis may be the results of Grossman’s (15, 16) experiments. He found that cholinergic stimulation of ventral amygdala evoked drinking but adrenergic stimulation evoked feeding in rats. On the other hand, Singer and Montgomery (41) and Mogenson (27), suggest that the amygdala may have only a modulatory influence on hypothalamic mechanisms of water intake.

Since classical studies of Anand and Brobeck (1) hypothalamus is considered as crucial structure for alimentary behavior, both positive (LH) and inhibitory (VMH). These authors in their pioneer experiments did not divide the mechanisms of food and water intake regulation.
Later, the results of experiments of Teitelbaum and Epstein (45) and Teitelbaum (44) undoubtedly showed that the rats recovering from lateral hypothalamic lesions usually regained their preoperative level of food intake much faster than that of water intake. These authors pointed out for the crucial role of the impairment of water regulation in the hypothalamic syndrome of aphagia.

Another possibility is that there may exist different anatomical substracts for water and food intake regulation as suggested by Robinson and Mishkin (36), Stevenson (42), Mogenson (26) and others. Sibole et al. (40) stated that the drinking behavior is regulated by septum (excitatory area being in medio-dorsal septum and inhibitory in ventro-lateral). Similarly Pizzi and Lorens (32) and Tondat and Almi (46) have found hyperdipsia after cutting of ventral connections of the septum (stria terminalis). On the other hand data obtained in the rats (3) and in the rabbits (31) demonstrated the existence of an osmoreceptive zone for thirst in the lateral preoptic area. These data were recently supported by electrophysiological experiments (49) as well as by anatomical data. It has been found (6), that the cortico-medial part of the amygdala has strong connections with ventromedial hypothalamus, basal part of the lateral nucleus of the septum and with, so called, medial preoptic — hypothalamic junction area. Similarly amygdalar afferents in the rat are originated mainly in anterior hypothalamus and medial preoptic area (5, 30) and from lateral septum (30). It might be suggested that this system may be at least partially the anatomical substract for the regula-tory mechanisms of water intake controlled by the medial part of the amygdala. All these problems need further investigations.

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Added in proof. Recently Box and Mogenson reported slight hypodipsia and hyperphagia after posterior ventromedial amygdala lesions.


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