

DIFFERENTIAL EFFECT OF VENTRO-MEDIAL AMYGDALAR LESIONS ON THE INGESTION OF DIFFERENT FOODS

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Abstract. The electrolytic lesions of the ventro-medial part of the amygdala in cats increased the cereal and milk intake and reduced the ingestion of meat. In consequence hyperphagia, hyperdipsia of milk and a significant increase of the total caloric intake developed only in cats fed cereal and milk. In cats fed milk and meat hyperdipsia and hypophagia, both of about 50% appeared, causing a small decrease of total caloric intake, and in cats receiving all kinds of food used in these experiments a similar depression in meat and increase in cereal and milk ingestion resulted only in a slight augmentation of caloric consumption. Thus, the ventro-medial amygdalar area controls the quality of the food ingested. It is suggested that the nutritional value of the protein component of the available solid food plays an important role. However, the intake of milk containing a high percentage of water seems to be independent of this regulation.

INTRODUCTION

It has been demonstrated in our previous experiments on cats fed milk, horse meat, boiled meat-cereal mixture and pure cereal (12, 15), that the lesions involving the area of junction of cortico-medial nuclei (Aco/Am), stria terminalis (St), and basal parvocellular nuclei (Abp), resulted in transient aphagia and adipsia followed by a long period of hypodipsia and selective aversion to meat, the intake of

which substantially decreased, contrary to the cereal intake. Electrical stimulation of this region increased the conditioned alimentary responses rewarded by meat (13), and daily intake of milk and a cereal-meat mixture (14). On these grounds the above area has been recognized as facilitating the feeding behavior in the cat.

On the other hand, our conclusion concerning the alimentary function of the basal, particularly of Abp nuclei, which have been defined as inhibitory, were based exclusively on the results of experiments during which the animals were fed milk and boiled meat-cereal mixture. Following lesions of these nuclei hyperdipsia of milk and hyperphagia developed while electrical stimulation caused a drop in milk drinking and in feeding (12, 14). These experiments do not determine whether hyperphagia resulted in an increase of appetite for both, or only for one of the mixture components. The clarification of this problem is the purpose of the present study.

METHOD

The experiment was performed on 34 adult cats of both sexes. Twenty four cats were divided into 3 experimental groups, 8 cats each, plus a control group consisting of 10 cats. All animals were given water and milk. Moreover, the cats of Group 1 received a cereal (boiled barley), the cats of Group 2 were fed raw and boiled horse meat cut into pieces and fish (mackerel in oil), and those of Group 3 and of the Control Group — both cereal and all kinds of meat mentioned above. Each kind of food was offered once a day in a separate bowl at 11 a.m. (for an hour *ad lib.*). The animals of Group 1 were preselected, because most cats refuse to eat cereal. The general behavior of cats during eating was observed. The body weight was checked once a week.

Bilateral electrolytic lesions of the amygdala were done with the use of the anodal direct current, 3 mA for 40 s. Lesions of the Abp nucleus were performed in the experimental groups and lesions of adjacent regions were done in the Control Group. The coordinates were taken from the Jasper and Ajmone-Marsan (5). The amount and sequence of ingested food had been measured for 6 wk before, and 6 wk after injuries. The localization of brain lesions was examined in paraffin sections stained with the Nissl's method. The results were subjected to a statistical analysis with the Mann-Whitney — *U* test (two-tailed).

RESULTS

Damage to the Abp nucleus

Pre-operative period. The cats of Group 1 which were fed barley ingested, on average, nearly one-third of solid food as compared to the cats of Groups 2 and 3. On the other hand, the intake of barley in cats of Group 1 was significantly higher than in Group 3 cats which were allowed a choice between meat and cereal (Fig. 1). The cats

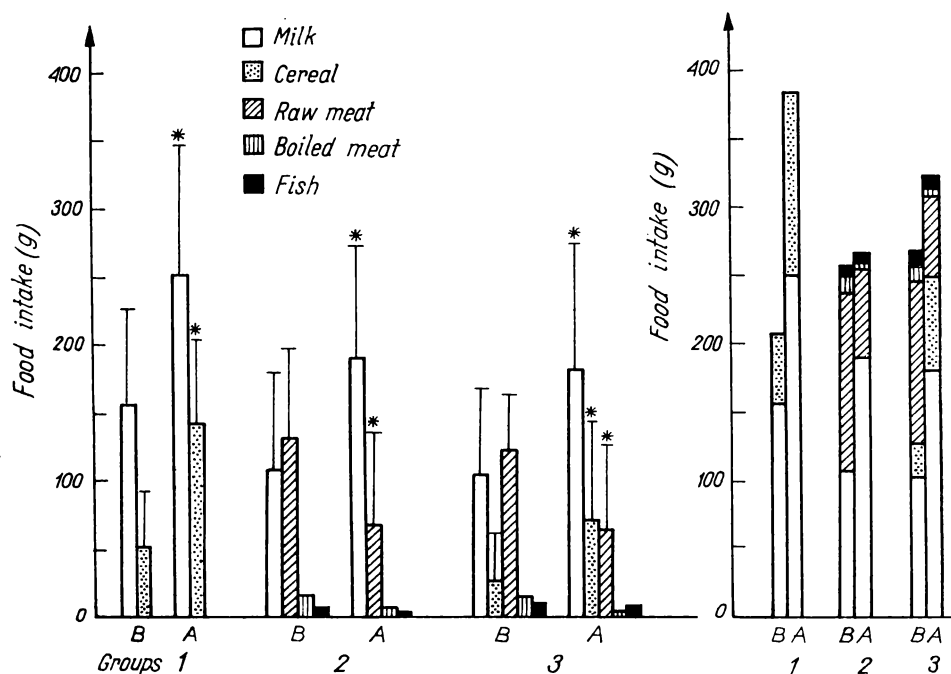


Fig. 1. Effect of ventro-medial amygdalar lesions on the food ingestion in three groups of cats receiving various diets, B, before injury; A, after injury. Left panel, intake of particular foods; right panel, total intake of milk and solid foods. Asterisks, $P < 0.002$.

refused to drink water, but all of them drank milk. The milk intake in Group 1 was higher by about 40% than in other groups. However, the caloric intake per kg body weight averaged about 40 kcal in Group 1 vs. about 52 kcal in Groups 2 and 3 (Table I). In a consequence, the cats of Group 1 lost about 8% of their body weight in the pre-operative period.

The amount of ingested nutrients was related to the intake sequence, i.e. most animals started their meals with food, which they

TABLE I

Mean caloric intake before (B) and after (A) operation

| | Group 1 | | Group 2 | | Group 3 | |
|---------------------------|--------------------|-------|---------|-------|---------|-------|
| | Total daily intake | | | | | |
| | B | A | B | A | B | A |
| | Milk | 82.5 | 132.8 | 56.5 | 100.5 | 54.9 |
| Cereal | 42.7 | 112.2 | — | — | 20.4 | 60.6 |
| Meat | — | — | 116.5 | 57.3 | 112.0 | 53.8 |
| | 125.2 | 245.0 | 173.0 | 157.8 | 187.3 | 208.8 |
| Intake per kg body weight | | | | | | |
| | 40.4 | 79.0 | 52.4 | 47.8 | 51.3 | 57.2 |

used to ingest in largest quantities. In Group 1 this was milk, in Groups 2 and 3 — raw horse meat.

Postoperative period. General observations. Lesions of the Abp nucleus evoked an intensified exploratory response consisting in sniffing the food before ingestion. Contrary to the pre-operative period, some cats were rather hesitant about the choice of their food, they sniffed one food, then another, they often picked up pieces of meat with their paws and threw them about. The intensity of these signs had gradually declined.

Meat intake (Groups 2 and 3). Two cats (in which the lesions were more medially localized) underwent a 4-day period of aphagia and adipsia. Both animals resumed spontaneous food intake on the 5th day. In some cats the quantity of ingested raw meat during the first meals did not differ from the amount eaten before injury, but on the following days the cats did not eat meat, and when they did again the intake was significantly reduced. On the average the meat intake declined in both groups by about 50% ($P < 0.002$), and this depression persisted until the end of the experimental period. The intake of boiled meat and fish also diminished by about a half (Fig. 1).

Cereal intake (Groups 1 and 3). Following the lesions of the Abp nuclei the intake of the cereal had increased, on the average, more than twice (Fig. 1). In some cats during the initial meals the increase was much higher. In one cat, belonging to Group 3, which ate very small amounts of the cereal in pre-operative period the increase during the initial post-operative meals was even tenfold. This was followed by a reduction of the intake of this food for 5 days more. After this initial period, the level of the cat's intake of the cereal had stabilized at a level three times higher than prior to surgery. In the Group 1 cats, the cereal intake was maintained at a fairly stable level during the

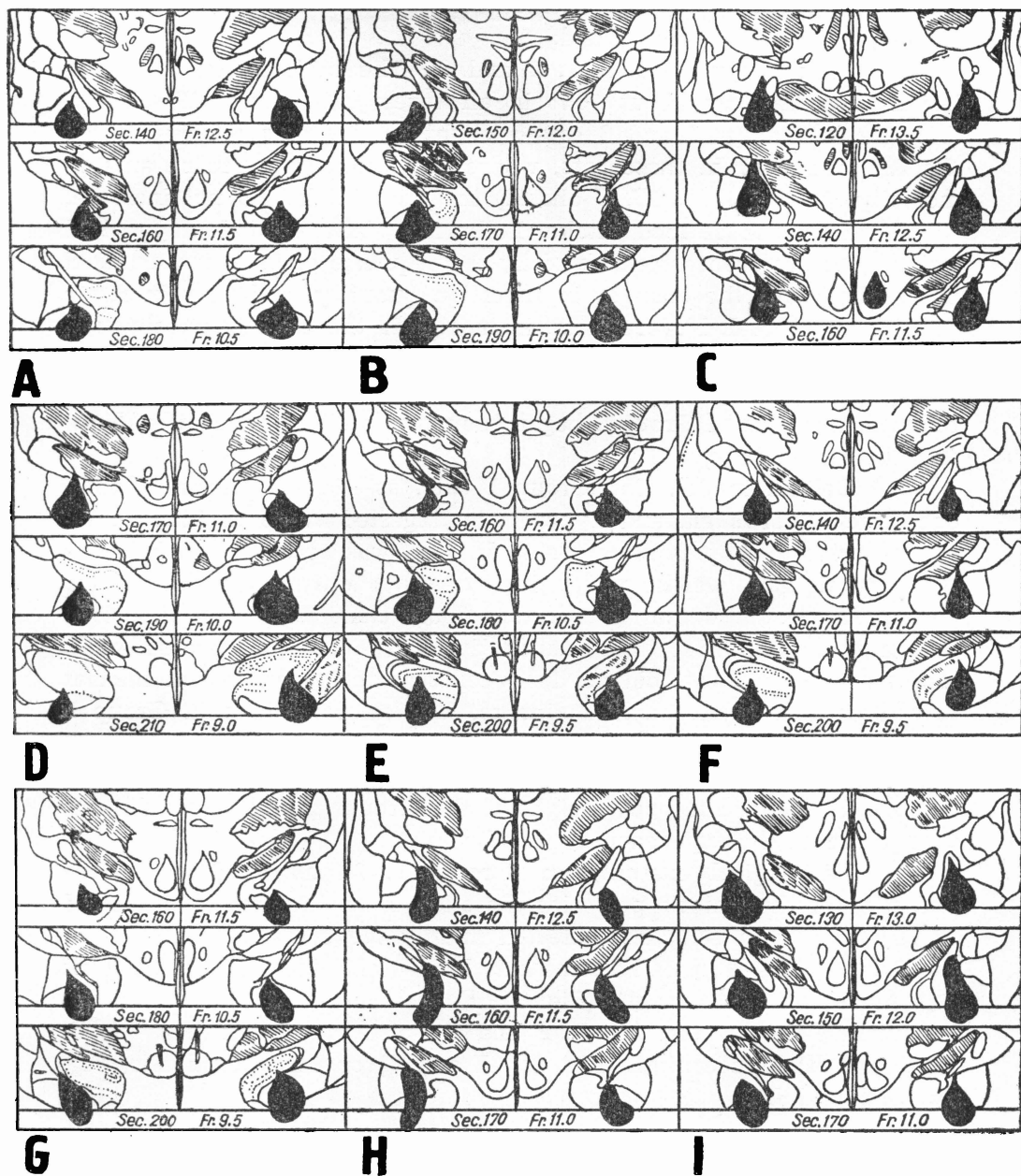


Fig. 2. Frontal sections of brains showing representative examples of lesions in the Abp nucleus which declined meat and increased cereal intake in Group 1 (A, B, C), Group 2 (D, E, F) and Group 3 (G, H, I).

whole post-operative period, whereas the Group 3 cats every few days, stopped eating and then resumed.

Milk intake (Groups 1, 2 and 3). The milk intake following lesions increased by about 70% in all three cat groups ($P < 0.002$) (Fig. 1). In Groups 2 and 3 cats a slight decline was observed from the 3rd week on. In three cats, where the lesions were more antero-medially situated (Fig. 2B, C and H) the milk intake did not increase.

Sequence of food intake. Following ventro-medial amygdaloid lesions, the preference manifested by the sequence of ingestion changed in parallel with the changes in ingestion quantity, and thus in favor of milk and cereal. Nevertheless, in most cats the ratio expressing the number of cases in which the animals began their meals with meat to cases when they began with other food was not inversed, but only reduced. The cats of Group 1 began their meals either with milk (50%) or with cereal (50%).

Caloric intake. The Group 1 cats, as a consequence of post-operative hyperphagia and hyperdipsia, ingested twice as many calories as prior to Abp injuries (Table I). This was accompanied by their tendency to gain weight which increased 8% during the observation period. In Groups 2 and 3 cats the global changes in ingesting food were rather qualitative than quantitative. However, the increased milk intake by Group 2 cats did not fully compensate for the loss of calories caused by the depressed meat intake. The caloric intake in Group 2 dropped, on the average, by about 9%, and in Group 3 due to the rise in both milk and cereal intake, the caloric intake increased on the average, by 12%. The body weight of the Groups 2 and 3 cats did not change during the experimental period.

Histological examination (Groups 1, 2 and 3). Most lesions extended in the antero-posterior direction from the frontal plane 9.5 to 12.0 (rarely to 13.0) and affected mainly the centro-medial part of the Abp nucleus (Fig. 2). In some cats lesions affected parts of adjacent regions of Aco or Am nuclei (Fig. 2C, E, G, H and I), basal magnocellular nuclei — Abm (Fig. 2C, D, F and G), piriform cortex (Fig. 2A, B, D, G and H) hippocampus (Fig. 2D, E and F) or Stria terminalis (Fig. 2C, E, F and H).

Damage to the adjacent regions

The intakes of milk, cereal and meat in the Control Group of cats were similar to those in Group 3. In three cats destruction of an area bordering on Abm nucleus, centro-medial nucleus (Acm) and St in the frontal plane from 10.0 to 11.5 (Fig. 3A) caused a significant

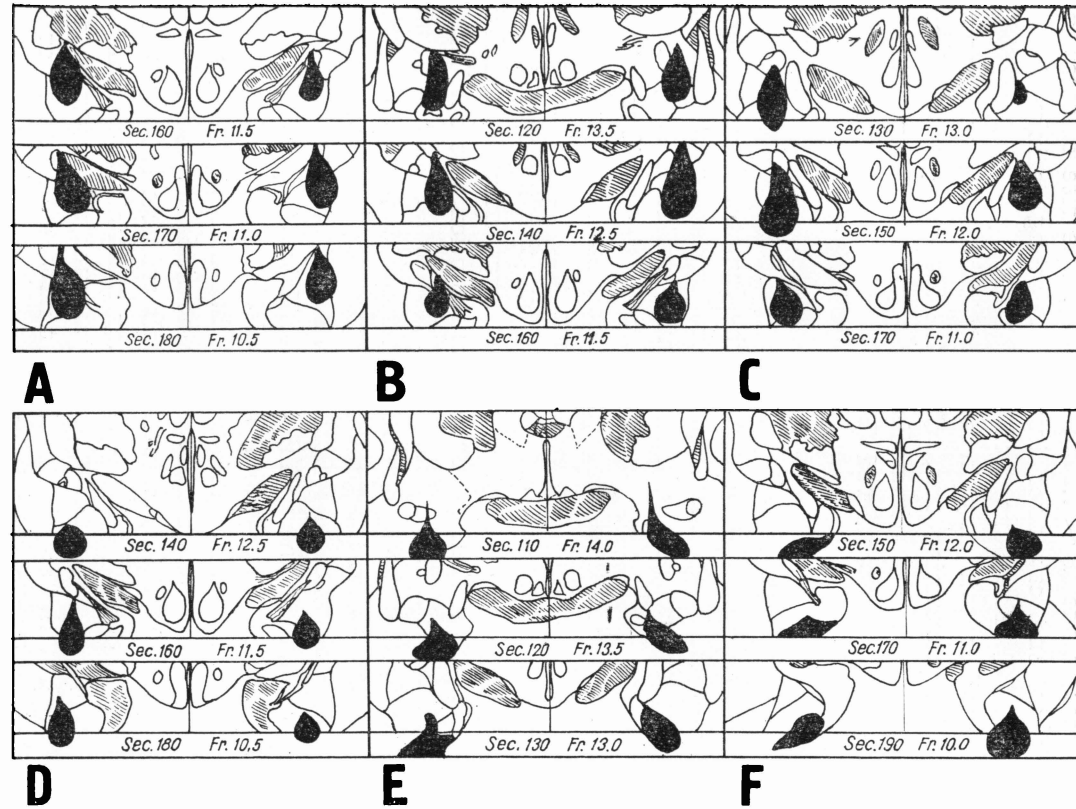


Fig. 3. Examples of various types of amygdalar lesions in the control group. Further explanations in the text.

rise of milk drinking ($P < 0.002$) and a total refusal of meat intake. In one cat similar injuries comprising Acn and Abm nuclei but localized more anteriorly, and damaging the Am nucleus rather than the St, caused an opposite effect, namely, a decrease of milk drinking and an increase of meat intake ($P < 0.002$); Fig. 3B). The rise of meat intake occurred also in one cat after injuries affecting mainly the Abm ($P < 0.002$; Fig. 3C). The damage of the centro-lateral part of the Abp resulted, in another cat, only in a slight increase of milk drinking (Fig. 3D). In four remaining cats, where the lesions comprised a part of the piriform cortex lying immediately beneath the Abp nucleus, no significant changes were observed (Fig. 3E and F).

DISCUSSION

In light of the present results, the hypothesis assuming that in cat the whole region of the Abp nucleus depresses the food intake (12, 13, 14) must now be modified. Ventro-medial lesions involving considerable part of the Abp nucleus induced three different effects depending on the kind of the diet. In general, the direction of changes in food intake observed in our experiments was very similar to that occurring after more medial lesions (15), but the increase in cereal intake after the lesions of the Abp nucleus was immediate and more pronounced, and the reduction in meat consumption was smaller.

The phenomena underlying these disturbances are not known, but there are observations which allow us to make some assumptions. One of them was proposed in the previous paper (15) and was concerned with the indirect influence of lesions on the food consumption through the presumed changes in the ACTH release. Now, the possibility of the amygdalar participation in feeding by a direct control of the protein component in the diet will be discussed. It has been proved that if the diet contains an adequate quantity of amino acids, vitamins, minerals and essential free fatty acids, mature animals are able to make a choice that satisfies their energetic needs and they maintain a constant body weight (4). On the other hand, when the amount of protein in a diet is too high or when the diet is deficient or imbalanced in one or more essential amino acids, the animals eat less, and lose weight (1, 2, 4, 8, 9, 18, 21). The diet offered to the Group 1 cats belongs to this last category. During preoperative period the cats from Group 1 ate about one-third of the solid food in comparison with the amounts ingested by animals from Groups 2 and 3. They partly compensated the nutrients deficiency by milk intake that was higher than in Groups 2 and 3. In spite of that, cats of Group 1 took fewer calories than the

cats of Groups 2 and 3, and this was accompanied by gradual loss of weight. It must be stressed that the cats of Group 3 allowed a choice between cereal and meat ate minimal amounts of cereal and their total intake of solid food did not differ much from that of Group 2 cats.

The dietary amino acid requirements of the cat are not known sufficiently; the subject has been only recently discussed in the literature (7, 16, 17, 19, 22). However, the content of some amino acids regarded as essential for the majority of adult animals as for instance that of lysine, arginine and methionine is significantly lower in the barley than in the meat. Methionine is just a limiting amino acid for barley. The essentiality of methionine for an adult cat was demonstrated recently by Teeter et al. (22) and that of arginine by Morris and Rogers (16, 17). Thus, both the low level of protein in the boiled barley and its amino acid imbalance might explain the depression in food intake and the loss of body weight observed in the Group 1 cats during the pre-operative period. Consequently, the increased cereal intake that we have obtained after lesions of the Abp nucleus shows that this part of the amygdala may be responsible for the depression effect displayed by cats fed a deficient protein diet. There is a strict analogy here with the results obtained in rats by Leung and Rogers (10, 11), who attribute the main role in this function to the anterior prepiriform cortex, but who have also stated that some lesions of the amygdala had alleviated the food intake depression effect of a diet imbalanced in essential amino acids.

The increase, in the milk intake in our experiments seems to be quite independent of the changes in the food intake. While the drinking of milk decreased after the ventromedial and anterior lesions (15), it increased after damaging the central part of the Abp nucleus and dorsomedial areas. However, the intake of meat decreased similarly in all these cases. Although the increase in milk drinking had compensated, to some extent for the deficit in protein intake, however, a full compensation of this deficit was never observed. We believe that the ingestion of milk, containing about 90% water, was regulated mainly as drinking response. It is worth mentioning that the lesions of similar regions in rats resulted in a similar rise of water intake (3).

As regards the decrease of meat consumption observed by us after Abp nucleus lesions it was not as drastic as after more medial injuries (15). Only in three cats with dorso-medial lesions the intake of meat dropped to zero. It may be assumed that in all cases discussed the same system was damaged. On the basis of the present experiments concerned only with a part of amygdala it is impossible to conclude about the extent of such a system.

Except for our previous studies on cats (12, 13, 15) there is no evidence in the literature that there exist in the brain some elements selectively facilitating the appetite for food being a rich source of full value protein with balanced pattern of amino acids. Because of a high requirement for protein in the diet of cats and presumably other felines (19), the existence of such a mechanism in these animals seems to be quite justified. Our results indicate that at least some parts of the amygdala in cats are responsible for the appetite for meat which prompts the animal to procure it.

In the investigation of the mechanism of the changes obtained by us, the possibility of impairment of either olfactory or gustatory discrimination should be rejected (6, 20). After the lesions, the animals had preserved their aptitude to differentiate food, displaying a definite steady tendency to changed preference and aversion to diets to which they had been previously accustomed. Moreover, we have stated that bulbectomy and destruction of the lateral olfactory tract and its nucleus in a cat fed such a diet resulted either in a long-lasting aphagia, or in a decline of the cereal intake, and an increased meat and milk ingestion, while tending to intensify the natural pre-operative preference (Lewińska and Olejnik, in preparation). No doubt, the animals with bulbectomy use the remaining unimpaired senses that may control diet discrimination.

The problem to what extent amygdalar preference and aversion are connected with previous alimentary experience still remains open. One of the possible hypotheses is that amygdalar neurons signaling need for nutrients get into associations with neurons informing about memory traces of the ingestive and post-ingestive sensory states related to given food, which leads to appetite for, or aversion to it, and sets the proper alimentary activity in motion. It is in accordance with Wyrwicka's (23) opinion that the need for nutrients can be satisfied practically only through the satisfaction of the need acquired by experience and related to definite stimuli.

Changes of food preferences appearing after amygdalar lesions which were of an emotional rather than basic gnostic character, would indicate a damage to this type of association. As a result, the rewarding aspect of one diet and the aversive aspect of the other, had abated simultaneously. The fact, that some cats consumed their first post-operative meal according to their primary preferences may suggest that, at the beginning, some previous peculiarities may have still persisted. The hesitation about the choice of their food and the careful sniffing that some cats displayed a few days after amygdalar lesions

might be an evidence of a conflict brought on by stimuli, which had lost their primary emotive meaning.

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