

THE EFFECT OF LATERAL HYPOTHALAMIC LESIONS ON GASTRIC MOTILITY IN DOGS

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Since the discovery of Anand and Brobeck (1951), the hypothalamus is considered as the main "food center". From this time many authors (Miller 1957, Wyrwicka 1957, Morgane 1961, Teitelbaum and Epstein 1962, Balińska 1963, and others) studied different aspects of the effects of hypothalamic lesions and hypothalamic stimulation on food intake mechanisms and conditioned reflexes in cats, rats, rabbits and goats. Among other alimentary functions the lateral hypothalamus exerts its influence also on the alimentary tract. The effect of electrical stimulation of the hypothalamus on gastric motility was described by several authors (Beattie and Sheehan 1934, Sheehan 1940, Eliasson 1952, 1954, Glavcheva 1964a, Fennegan and Puiggari 1966, and others). We have much less informations concerning the effect of the hypothalamic lesions on the functions of the alimentary tract. It seems that Mayer and Sudsaneh (1959) were the only ones who performed this kind of chronic experiment on rats. They did not find, however, any effect of the lesion on gastric functions.

From the recent work of Rożkowska (1969) and Rożkowska and Fonberg (1970) it is known that lateral hypothalamic lesions impair various alimentary functions in dogs. After the operation these animals were not only aphagic or hypophagic but also their instrumental conditioned reflexes were deeply impaired. In addition, in all the animals persistent vomiting was observed (Fonberg 1968, Fonberg and Rożkowska 1968). In rats and cats this symptom was not previously described by other

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authors as the part of the hypothalamic syndrome. It may be supposed that vomiting is produced by changed activity of the stomach, i.e. increased contractions of its musculature, which in consequence may produce the ejection of food or nausea. As shown by Babkin and Kite (1950a) after hypothalamic lesions performed under anesthesia, the rate of stomach contractions increased from 3/min to 5/min or more. In this respect, lack of appetite after hypothalamic lesions (at least one part of the mechanism involved in this syndrome) may be referred to the state of nausea and explained by the changes in sensory input from the periphery.

The aim of the present paper was to study how the lesion of the lateral hypothalamus affects the motor functions of the stomach during various phases of the alimentary act, and conditioned alimentary reflexes on dogs.

MATERIAL AND METHODS

The experiments were performed on four male mongrel dogs 12-14 kg of weight, called Fafik, Dudek, Morus and Nero. In aseptic conditions under Nembutal anesthesia (35 mg per kg) a gastric fistula was made whose walls were formed from the fragment of colon transversum according to the Glavcheva method (1964b).

A few weeks after the fistula operation, daily experiments in a standard Pavlovian CR chamber were initiated. First, the animals were fully accustomed to stay quietly on the Pavlovian stock in a standing position, being on a leash and in a harness. They learned to take food from the bowls in a feeder 14 cm high, situated in front of the animal. Each portion of food consisted of 50 g of dry biscuits, in cubes of the size of about 8 cm³, mixed with minced boiled meat. They were also accustomed to the procedure of recording the stomach activity. To this end, before the animal was brought to the experimental situation his stomach was carefully rinsed by water of room temperature, and all the remnants of food left after the previous feeding were removed. After the animals were placed on the stock, a rubber balloon was introduced into the stomach, filled with air, and connected with the recording system located in the pre-chamber on the experimenter's desk. The experimenter observed the dog through a one-way window. After each session which lasted usually from 30-60 min the dogs were taken to the animal house, and after 2-4 hr fed with his routine meal (cereal with broth and meat). In these conditions, each session took place after 18-22 hr of feeding (the details of the elaboration of the conditioned reflex were described previously, Glavcheva et al. 1969).

A few weeks after the operation the CR experiments started on three dogs and they lasted for two months or longer. One dog, Nero, was not trained in conditioned reflexes before the hypothalamic operation. The training sessions consisted of four trials separated by about seven-minute intervals. The conditioned stimulus was the sound of a metronome, 80 beats per min, which lasted for one minute. After 50 sec of its action the food was presented, the act of eating continuing for 30-60 sec.

When the conditioned reflex to the metronome was firmly established, brain lesions were performed under Nembutal anesthesia (35 mg per kg) by means of

d-c pulse (3 ma) lasting 1 min. The electrodes were stainless steel needles 0.5 mm in diameter insulated by enamel except for 0.5 mm at the tip. Electrodes were placed stereotaxically and aimed at the lateral part of the hypothalamus, according to the coordinates based on the Atlas of Lim et al. (1960).

Regular testing sessions were started 10–14 days after the operation when the dogs were able to take the food from bowls. The dogs were under observation for 2–3 months, or longer.

After the experiments were accomplished, the dogs were sacrificed and their brains perfused with 10% formalin. Then, the brains were embedded in paraffin and sectioned frontally at 20 μ . Every tenth section was stained by the Klüver or Nissl method alternately.

RESULTS

Food intake and general behavior

In all the dogs aphagia was observed. It lasted in Fafik two days, in Dudek four days, in Morus ten days, and in Nero twelve days. During this period the dogs were fed artificially by gastric intubation and forced feeding. Afterwards the state of hypophagia was observed which lasted 2–3 weeks. In this stage although the dogs started to eat the food voluntarily, they had to be baited to start eating, and they consumed much less food than before the operation, showing food preference.

On the first day after the operation, vomiting appeared. In the period of aphagia all the dogs vomited as a rule after each feeding. Later, during hypophagia vomiting was also observed, usually appearing in 15–20 min after meals. In two dogs, Morus and Nero, vomiting appeared regularly after meals in the first weeks after the operation, and persisted till the end of the observations. In the two other dogs after the period of aphagia vomiting was observed only sporadically.

The dogs' general behavior was also greatly changed; the activity of the dogs diminished, with apathy and somnolence prevailing. In the first few days after the operation in Morus and Nero strange "cataleptic-like" postures were observed.

The stomach activity

In the period of aphagia the motor activity of the stomach was only occasionally checked because the dogs were atonic. They dropped on the leash and could not bear long periods of standing on the stock. In this stage it was observed that the stomach activity was markedly disturbed, stomach contractions ceased, the tonus decreased and atonia prevailed. Particularly persistent and longlasting atonia occurred in Morus and Nero; it lasted about six weeks in Morus and five weeks in Nero (Fig. 1). In Fafik and Dudek we did not observe atonia but rhythmic,

regular automatic contractions of a tonic character and with a frequency of about 5/sec, which had never appeared before the operation (Fig. 1). In Morus and Nero the tonic contractions also were sometimes noticed but only in the late postoperative period.

Starting from about the 4th week in Fafik, and the 6th week in Dudek the motor activity of the stomach began to recover. In Morus and Nero which were under observation for 3–4 months their stomach motor activity was not fully recovered until the end of the experiments and the lability of stomach activity was always observed.

It is interesting to note that in parallel with the recovery of normal basic activity of the stomach, periods of hyperactivity of the stomach motility were observed in all dogs (Fig. 2). It took the form of high amplitude contractions 2 or 3 times higher than before the operation.

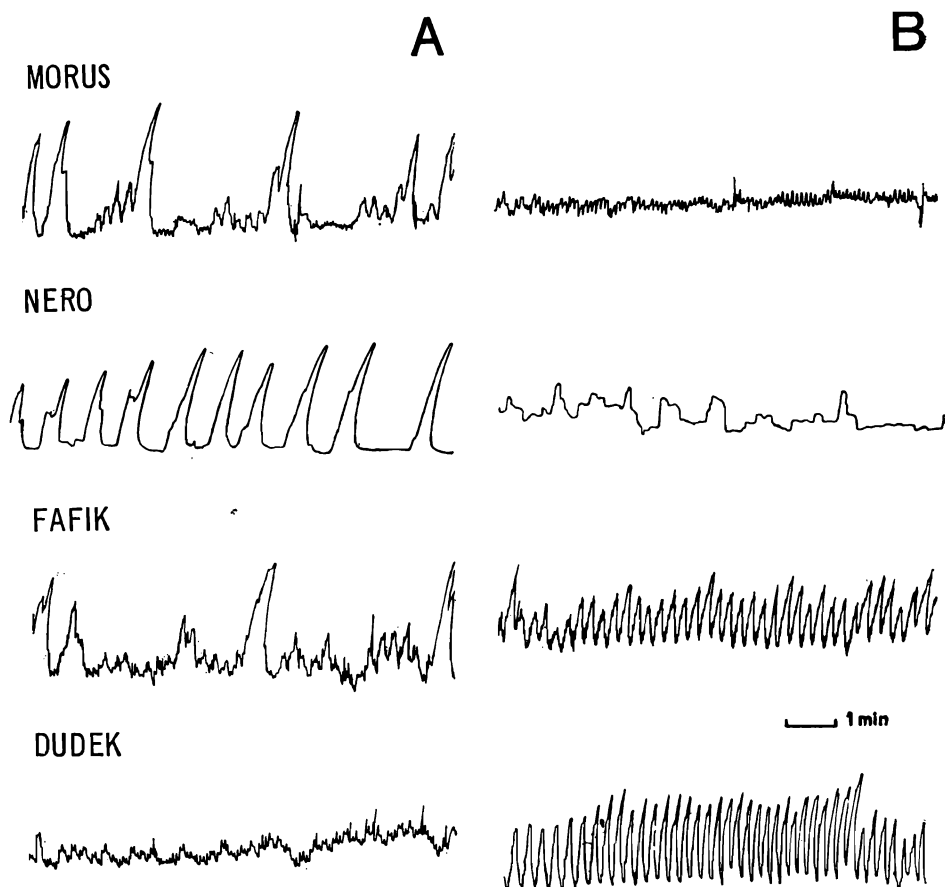


Fig. 1. Typical records of the motor activity of the stomach before (A) and after (B) lateral hypothalamus lesions.

Most frequently these periods of hyperactivity occurred in Nero, i.e. in the same dog in which atonia was the most pronounced during the first five weeks after the operation. In general, the stage of recovery presented a multiform picture of stomach activity. Atonia, periods of tonic contractions, and hyperactivity were observed, occurring in no systematic order. This chaotic activity being in particular true for Nero and Morus.

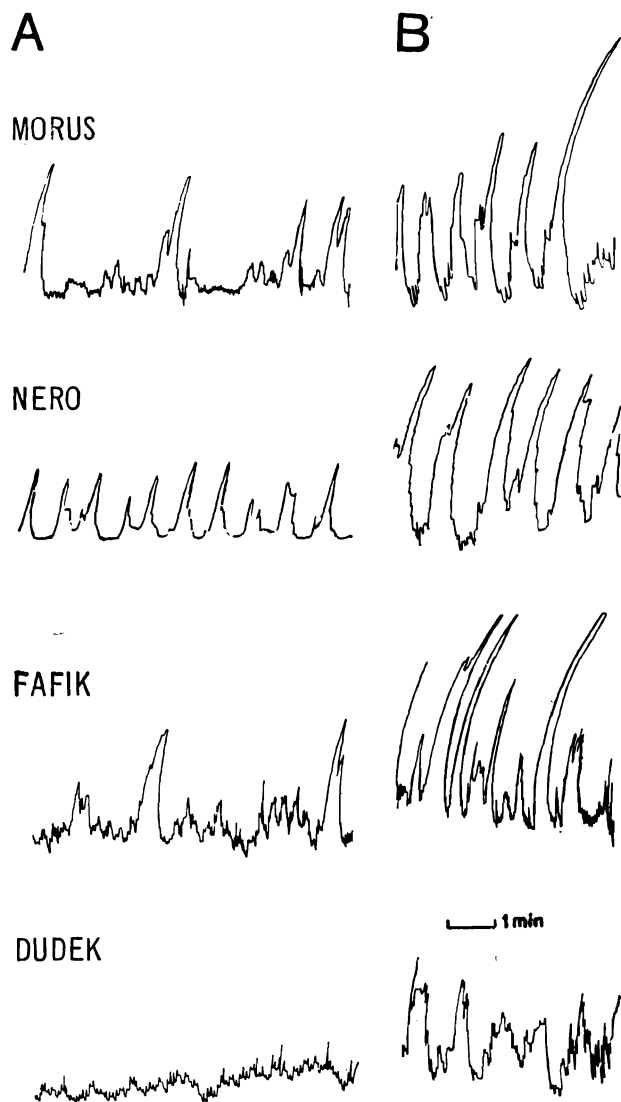


Fig. 2. The postoperative periods of hyperactivity of the stomach (B) as compared with normal preoperative activity (A).

*Stomach activity in response to the conditioned stimulus and
unconditioned stimulus*

During the first experimental sessions after the operation the dogs did not react to the metronome sound and were not interested in food. Often they had to be encouraged to eat.

In the preoperative period the application of the conditioned stimulus in the first trial, i.e. when the stomach was empty, produced a marked relaxation of the stomach wall's tonus and inhibition of the stomach

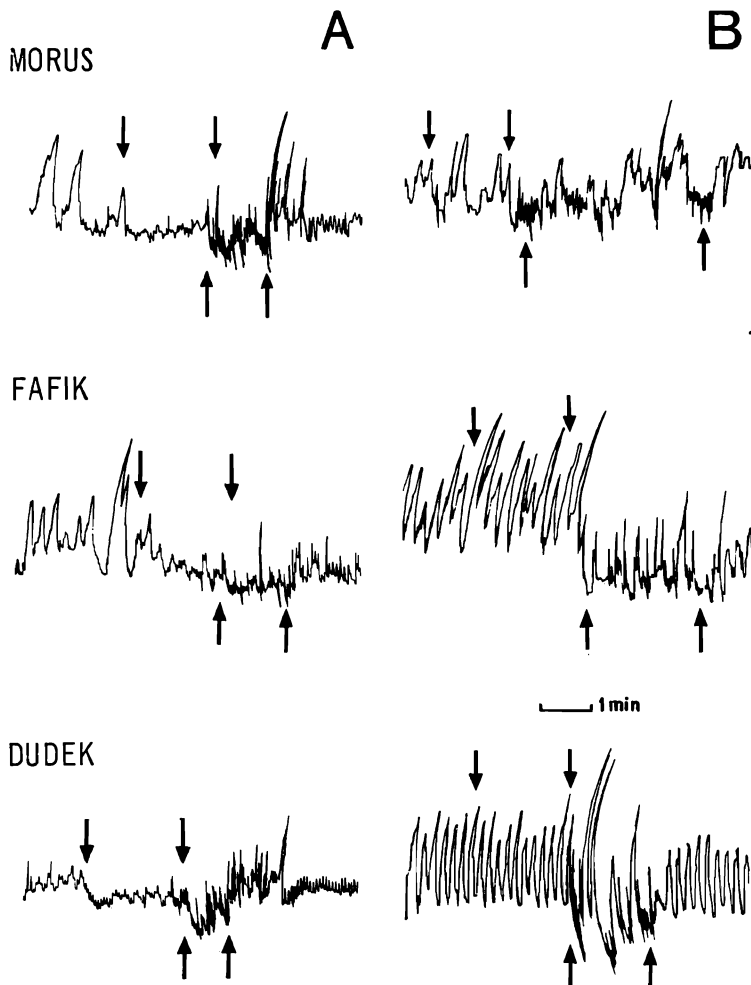


Fig. 3. Conditioned alimentary reflexes before (A) and after (B) the operation. Notice the lack of the conditioned relaxation after the operation (B). Duration of the conditioned stimulus between upper arrows, unconditioned stimulus—food intake between lower arrows.

contractions (for details see Glavcheva et al. 1969). In the postoperative period we did not notice any effect of the CS on the motor activity of the stomach (Fig. 3). Also the characteristic syndrome occurring preoperatively, i.e. receptive relaxation in the response to food reaching the stomach, was not marked after the operation. The period of food intake was two- or three-fold prolonged in comparison with the normal time of eating this last symptom being probably caused by clumsy mastication.

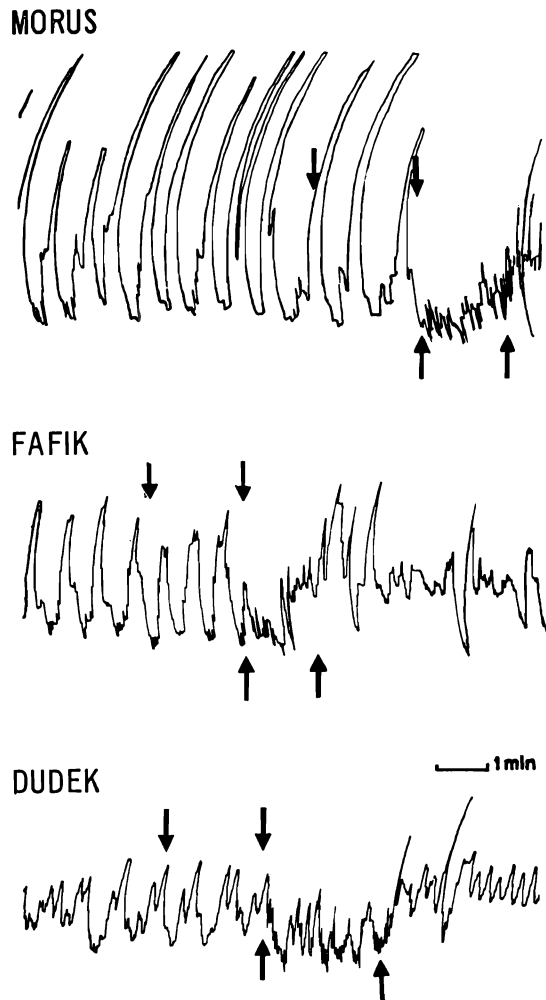


Fig. 4. Conditioned reflexes during hyperactive phase after the operation. Duration of the conditioned stimulus between upper arrows, unconditioned stimulus—food intake between lower arrows.

Several weeks after the operation the gradual restoration of the conditioned reaction occurred. The effect of the conditioned stimulus, first appeared in dog Fafik as a slight decrease of tonus. The first sign of conditioned reaction was noticed in this dog in the 5th week after the operation. In Morus this appeared later, i.e. in the eight week after the operation (Fig. 4). In Dudek, in spite of the fact that the basic motor activity of stomach reappeared rather early, we did not observe any conditioned effect of the conditioned stimulus.

In all dogs the application of the conditioned stimulus on a background of stomach hyperactivity failed to evoke the conditioned relaxation effect or a decrease in the contraction amplitude (Fig. 4).

Anatomical verification

In all dogs the lateral hypothalamic area in the tuberal part was destroyed as the effect of the electrocoagulation.

In two dogs, Nero and Morus, the lesions were very similar, i.e. they were extensive, bilateral and extended from the fornix region laterally and beneath it damaging also the most ventral part of the internal capsule. In Nero the lesion destroyed almost the whole lateral hypothalamic area extending down towards the tractus opticus without damaging it however. In Morus the lesions destroyed also the lateral hypothalamus bilaterally, covering the same area as in Nero except for the lowest part

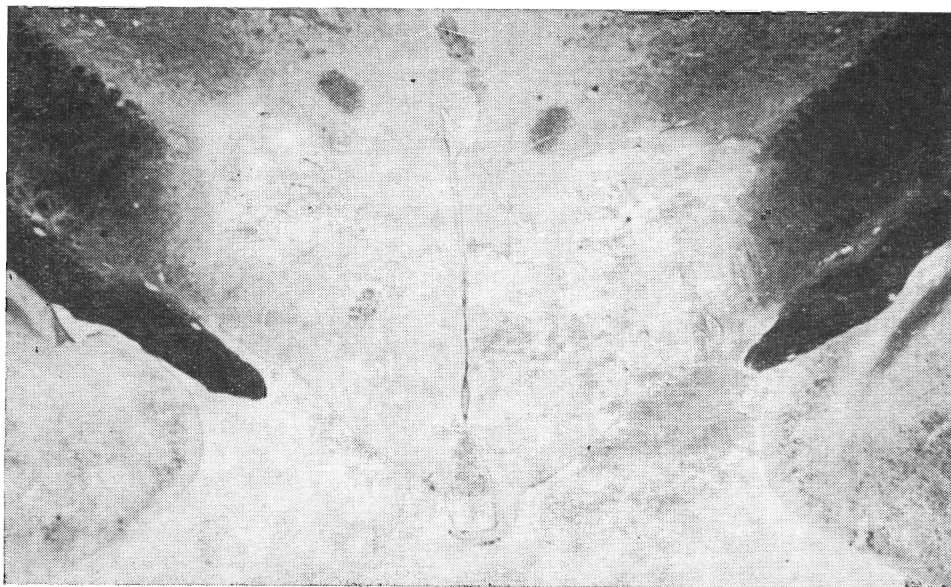


Fig. 5. Representative frontal section of the brain of dog Morus showing a typical extensive symmetrical bilateral lesion in the lateral hypothalamus.

(Fig. 5). In Fafik the lesion was symmetrical, bilateral, and limited to the superior part lateral hypothalamic area, reaching as far as the boundary between the hypothalamus and thalamus. The inferior part of the lateral hypothalamus remained undamaged. In Dudek on the right side the lesion covered the lateral hypothalamic area exceeding beyond it and reaching the medial part of the hypothalamus; on the left side only lateral hypothalamic area was destroyed.

DISCUSSION

The results of our experiments show that lesions situated in the lateral hypothalamus not only impair the food intake ability of the dogs and produce changes in their general behavior and instrumental reactions, as has been previously described by Rożkowska (1969) and Rożkowska and Fonberg (1970) but also evoke deep changes in the motor functions of the stomach.

This seems to indicate that the role of the lateral hypothalamus in respect to alimentary functions is quite general and it is not limited to mediating the motivational and instrumental functions of feeding behavior, but concerns among others also the functions of the stomach. This is in agreement with Eliasson (1952) and Fennegan and Puiggari (1966) who showed that lesions or stimulation of the hypothalamus affect the motor functions of the alimentary tract.

It is interesting to note that the lateral hypothalamic lesions impair various aspects of the motor activity of the stomach. In the previous work (Glavcheva et al. 1969) the several phases of the stomach's functions during the process of conditioning was described. According to Konorski's hypothesis (1967) the regular periodic contractions of the stomach are the effect of the hunger-drive, and the relaxation of the tonus both conditioned and unconditioned are considered as the indication of the consumatory reflex. After lateral hypothalamic lesions both hunger contractions and relaxation effect became impaired. This shows that it is difficult to divide, by our present methods, the consumatory and drive functions of the stomach at the level of hypothalamus. The same conclusion follows from the previous work of Fonberg (1966, 1967) who showed that stimulation of the same loci in lateral hypothalamus both produces food intake in satiated dogs and serves as the reward for the instrumental training.

Our experiments were performed on only a few dogs, and although in all of them the lateral hypothalamus was impaired, the location and dimensions of the lesions differed in particular subjects. Therefore, our

work has only a preliminary character and on this basis it is not possible to discuss the general role of the lateral hypothalamus. As far as our results show we may point out only the fact that several motor functions of the stomach are impaired by hypothalamic lesions, although not in the same degree.

In the first period after operation the basic motor function, reflected in periodic, regular contractions is impaired. The stomach is atonic or shows rhythmic, automatic contractions. In this stage no unconditioned or conditioned reflexes can be evoked. This basic activity is the first which became restored. The conditioned reflex reappeared the last.

It is worth pointing out that the changes in motor activity of the stomach parallel all other symptoms comprising the "lateral hypothalamic syndrome". Just after the operation, i.e. in the period of aphagia and apathy, the state of the animals did not allow us to perform regular experiments. Nevertheless, the data of sporadic observations show unequivocally that the stomach was in complete atony. The regular experiments started 10–14 days after the operation, when the dogs began to eat spontaneously but still showed hypophagia. They had to be baited to take food, they were uninterested in the environment and hardly reacted to the external stimuli. Gastrogrammes taken during this period showed atony and lack of periodic contractions. In two dogs, Fafik and Dudek, which were not so depressed as the other dogs, tonic automatic, regular contractions of low amplitude were registered. In the two other dogs tonic contractions appeared later after the period of complete atony. Both atony and tonic contractions may be explained by the same mechanisms, i.e. lack of impulses from the hypothalamus.

Tonic contractions may be caused by the pressure of the balloon on the stomach wall and consist in a peripheral reflex (mediated by the Auerbach and Meissner's ganglia situated into stomach's wall), which is normally inhibited by the CNS. After the hypothalamic damage this reflex is liberated from the central inhibition and may be activated. Similarly, the lack of the "hunger" contractions may be explained by the cut-off of the influences from the CNS.

According to Carlson (1916) the periodic contractions reflect the state of hunger and according to Quigley (1955) the desire for food (appetite) closely parallels the hunger contractions. This conclusion is based on the experiments of many authors (see also Quigley 1955). In this light it is understandable that the lateral hypothalamic lesions which produced aphagia and lack of alimentary motivation abolished also the gastric contractions.

Several authors have pointed out that "hunger" contractions are mediated through n.vagus. In the lower vertebrates, for example frogs,

in which vagus is not developed, the "hunger" contractions are not observed (Belenikaya 1956). In the higher species, after the section of the n.vagus the regular "hunger" contractions disappear, and the stomach activity becomes persistent and automatic. The regeneration of the vagus in the first stage evokes the inhibition of automatic contractions, and later periodic contractions are restored (Tetyaeva 1947). This author stressed the role of the n.vagus in the inhibition.

On the other hand, according to Hesser and Perret (1960) the inhibitory impulses for the motor function of the stomach are mediated through sympathetic system. This point of view has been widely accepted. Kaada (1951) showed that after vagotomy both inhibitory and excitatory effects of the stimulation of the cortex are abolished, which facts brought him to the conclusion that n.vagus has double (inhibitory and excitatory) representation in the cerebral cortex. Babkin and Kite (1950ab) discuss the possibility of the inhibitory influences of the cerebral cortex on the centers of n.vagus. The dual role of the n.vagus may be explained by results of Jansson and Martinson (1965) who showed that in the trunk of n.vagus there exist two kinds of efferent fibers, which differ in their excitability threshold. The fibers with low threshold mediate the contractions and the fibers with high threshold of excitability transfer impulses for relaxation of the gastric muscules. Later, Fennegan and Puig-gari (1966) observed that both the inhibitory and excitatory effects produced by the stimulation of lateral hypothalamus disappeared after section of the n.vagus.

Our experiments demonstrated clearly that lesions of the lateral hypothalamus impair in the first stage after the operation "hunger" contractions, i.e. the excitatory influences, as well as the relaxation effects both conditioned and unconditioned. These last may be considered as an inhibitory effect. In this respect, lesions of the lateral hypothalamus have very similar results as the section of the vagus, and therefore it may be concluded that most of the hypothalamic control over gastric motility is mediated through n.vagus.

After 3-4 weeks post operation gradual compensation is noted. First restored was the basic function of the stomach, and periodic contractions reappeared. At first, the recovery was very labile and the periods of normal and disrupted activity interchanged. Later, the unconditioned relaxation as the reaction to the food reaching stomach reappeared, and the conditioned relaxation was the last to reappear.

It is interesting to note that in this period after the operation, when the general behavior of the dogs became activated, motor activity of the stomach is also activated, sometimes taking the form of hypercompensation expressed in periodic "hunger-like" contractions with very great

amplitude to an extent never observed before the operation (see Fig. 2 and 4). It may indicate that other brain structures which play a role in the recovery of alimentary functions, are overexcited and the balance between excitatory and inhibitory impulses is not yet elaborated, leading to increased motor activity of the stomach.

The total recovery of the functions is not observed, however, until the end of the experiments (3–4 months). The degree of recovery differs in particular dogs depending on the lesioned areas of the lateral hypothalamus. Dog Fafik has a very small lesion situated dorsally to the main "alimentary center". In this dog the periodic contractions appeared rather early, after about four weeks after operation and the traces of the conditioned reflex appeared in the 5th week after the operation. Dudek had lesions not quite symmetrical, and in consequence on the right side the great part of the lateral hypothalamus was spared. In this dog the basic function of the stomach also reappeared rather early (6 weeks after the operation). The most extensive lesions, involving almost the whole lateral hypothalamus were found in dogs Nero and Morus, and in these dogs the recovery was very labile and the changes in basic motor function were observed until the end of the experiments. Also, the general behavior of these dogs was greatly changed and did not attain its preoperative state.

It is difficult to explain, however, the complete lack of the conditioned relaxation effect on dog Dudek in which the basic activity reflected in hunger contractions was restored in six weeks, and whose general behavior did not differ from the normal after a few months. Nevertheless, the conditioned reflexes did not reappear, in even changed or diminished forms, until the end of experiments.

It remains to be explained whether the vomiting, which is regularly observed as the result of the hypothalamic lesion may be caused by the changed stomach activity. The vomiting reflex is also mediated by n.vagus. If the effect of the lateral hypothalamic lesions on the stomach activity were similar to the effect of vagal section, the opposite effect should rather be expected i.e. — abolishment of the vomiting-reflex. On the other hand, as a result of hypothalamic lesion the receptive relaxation after food intake does not appear, but instead the muscles of the stomach are tonically contracted. This may be the factor producing nausea and in consequence vomiting. The amounts of the food which served as the reinforcement during each trial of the experimental session were very small, therefore we did not observe vomiting after each trial. It appears though very often after the end of experimental sessions and regularly after the normal meal in the home cage.

As shown by French et al. (1953), Misher and Brooks (1966) and

others the acidity of the stomach juice is greatly changed during hypothalamic stimulation. It is possible that these two factors: lack of receptive relaxation and changed acidity may produce vomiting. This problem needs, however, additional studies to be fully elucidated.

SUMMARY

The effect of lateral hypothalamic lesions on the gastric motility of dogs was studied. It was found that: (i) After the operation the periodic "hunger" contractions were abolished, the stomach was completely atonic or showed automatic tonic contractions. (ii) Both conditioned and unconditioned relaxation effects were also completely abolished. (iii) After some weeks partial recovery occurred. First restored was the basic activity reflected in periodic contractions. Later unconditioned relaxation appeared and the conditioned relaxation was the last to be restored. In two dogs, until the end of experiments the conditioned reflexes were not fully restored. (iv) The possible mechanisms of this phenomenon and its relation to the function of the n.vagus were discussed.

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