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QUALITATIVE VERSUS DIRECTIONAL CUES
IN DIFFERENTIAL CONDITIONING

IV. LEFT LEG-RIGHT LEG DIFFERENTIATION
TO NON-DIRECTIONAL CUES

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In a preceding paper of this series (Dobrzecka and Konorski 1967) it was shown that if the left leg-right leg differentiation is established in a dog on the basis of both qualitative and directional cues, the animal consistently utilizes the latter cue totally neglecting the former one. Therefore the problem arose as to whether the same task can be mastered in the case in which the two differentiated stimuli operate from the same place, a circumstance which does not allow the animal to take profit of the orienting reactions towards the sources of the stimuli. In the present paper we are concerned with this problem.

MATERIAL AND METHODS

The method applied in the present study was in general the same as that in the preceding paper (Dobrzecka and Konorski 1967). The experiments were performed on dogs in a soundproof CR chamber. The animal was placed on the stand with the feeder situated to the front. Two indifferent stimuli denoted as S_R and S_L were presented in random order with the intervals of about one minute. Five seconds after the onset of the stimulus S_R the right foreleg of the animal was passively bent and placed on the feeder. This was done by a technician pulling a string attached to the wrist of that leg. Immediately afterwards the bowl with food was put into position. When stimulus S_L was presented the passive movement

of the left foreleg was produced by the same procedure. Eight or nine trials were given in each experimental session with random distribution of the two stimuli.

After a few sessions the animals started occasionally to perform actively the required movements during the operation of each CS. If the movement was correct it was immediately followed by food, if not, the CS was discontinued and food not presented. If no active movement was performed by the animal during the five seconds operation of the CS, the appropriate passive movement followed which was reinforced by food.

The following varieties of experiments were performed:

Variety 1 (2 dogs). As in the preceding series (Dobrzecka and Konorski 1967) S_R was the beating of a metronome (M) and S_L was the sound of bubbling water (B), however, in contradistinction to that series, the apparatuses producing these sounds were situated close to one another in front of the animal.

Variety 2 (5 dogs). Two tones were produced from a generator placed in front of the animal. S_R was the tone of 1500 c/sec (T_{1500}). S_L was the tone of 300 cps (T_{300}).

Variety 3 (3 dogs). In these experiments S_R was lightening of the lamp, S_L was bubbling of water. Both stimuli were presented from the front of the animal.

RESULTS

Part I

Variety 1 (M-B differentiation). The whole course of training with one of the two animals used in these experiments is presented in Fig. 1a. For the sake of comparison a typical course of differentiation of M and B sounding from different sources (Dobrzecka and Konorski 1967) is presented in Fig. 1b.

Comparing the two courses of training the clear difference between them is manifest. In the case when directional cues were presented the animals reached the 100% correct performance after two 80-trial blocks. On the other hand, when both CSs operated from the same place the differentiation training appeared to be exceedingly difficult and required no less than fifteen 80-trial blocks. Since the course of this training was similar for both dogs trained in this way, it can be described jointly.

Not taking into account the first 80-trial block in which the animals learned to perform actively the trained movements, the whole training may be divided into two periods. In the first period, including about six 80-trial blocks, both animals accepted the following strategy: in most instances they performed the correct movement (lifting the left foreleg) in response to bubbling and only occasionally did they make the incorrect movement of the right foreleg. On the other hand, in response to the metronome they performed the same movement as in response to bubbling, which was of course, not reinforced by food. Because of this the active movement to the metronome was soon extinguished and in most instances the dogs simply did not perform any movement in response to

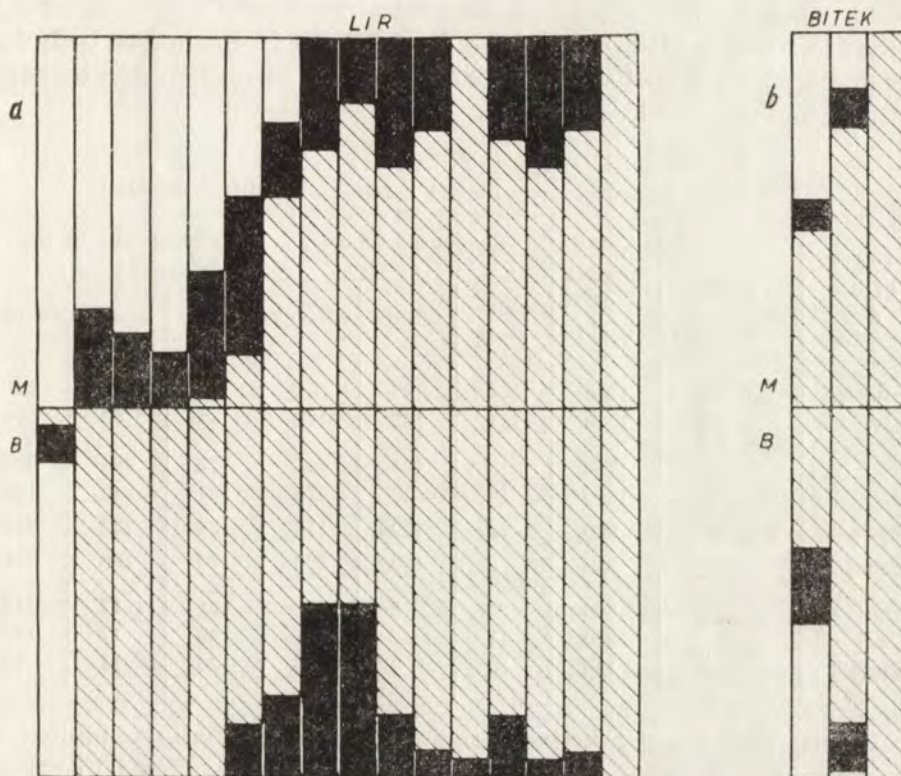


Fig. 1. Formation of the left leg-right leg differentiation to non-directional cues (a) and to directional cues (b) in two different dogs. Each column represents 40 trials. Columns below the middle line denote bubbling trials, those above the middle line denote metronome trials. White parts of the columns denote those trials in which passive movement was provoked; hatched parts denote those trials in which active correct movement was performed; black parts denote trials in which wrong movement was performed. Note the very prolonged training in a, and very quick training in b. Note also a long series of metronome trials in which no active movements were performed

this stimulus, but they waited till the right foreleg was passively lifted and then food presented.

Since such a situation remained unchanged for almost 500 trials, it seemed to be hopeless. However, after this lengthy period the situation changed in one dog gradually and in the other almost abruptly. The animals began to lift the right foreleg more frequently than before, performing this movement not only to the metronome but also to bubbling. Accordingly, the number of errors to the latter CS strongly increased. Nevertheless it may be observed that the general number of correct responses was above the chance level, showing that both animals had

found a cue by which the task should be mastered, not being able to utilize this cue in all the trials. Gradually the performance of both dogs became better and better, and eventually, after more than one thousand trials, it became errorless (Table I).

Table I
The performance of dogs in left leg-right leg differentiation

Name of the dog	Task	Total number of trials	Responses to S_R			Responses to S_L		
			no resp	wrong	correct	no resp	wrong	correct
Pucek	M→R	1240	251	85	284	22	61	537
Lir	B→L	1200	184	142	174	34	62	504
Śmiały		1760	15	423	442	27	291	562
Fifek	T_{1500} →R	1080	46	18	476	169	242	129
Borsuk	T_{300} →L	920	22	120	318	24	124	312
Żabot		920	9	169	282	23	186	251
Znajda	L→R	360	22	8	150	21	17	142
Czuj	B→L	360	17	12	151	20	17	143
Rudzik		180	30	4	56	26	11	53

During this lengthy training the animals occasionally exhibited all the symptoms of subneurotic states: they were restless, tried to get out of the CR chamber, and refused to take food from the feeder.

Variety 2 (T_{1500} - T_{300} differentiation). These experiments were performed on 5 dogs, one of them was, however, discarded because he developed a severe neurosis and became unmanageable. The results of the experiments on the other dogs are presented in Table I, and the illustration of the course of training is shown in Fig. 2 and 3. It may be seen that the task the animals were confronted with, seemed to be for a long time insoluble. The difference between this group and the preceding one was that the animals had a stronger tendency to perform active movements (right or wrong) to both stimuli, that is, the long series of no responses to one of the CSs was absent. This was probably due to the stronger generalization between the two tones than between the metronome and bubbling. Whereas two dogs (Borsuk and Fifek) eventually solved the task (Fig. 2), the two other ones (Żabot and Śmiały) seemed to be hopeless (Fig. 3). In view of this fact it was decided to change the procedure in these dogs by presenting one of the tones (1500 cps) from the front and the other tone (300 cps) from behind. As is seen in Fig. 3b this measure brought a nearly immediate success and after about 120 trials the task was solved. It is interesting to note that when

afterwards in *Žabot* we returned to the original training, the two tones being produced from the front of the animal, the task has been eventually mastered and the dog succeeded in achieving the nearly errorless differentiation.

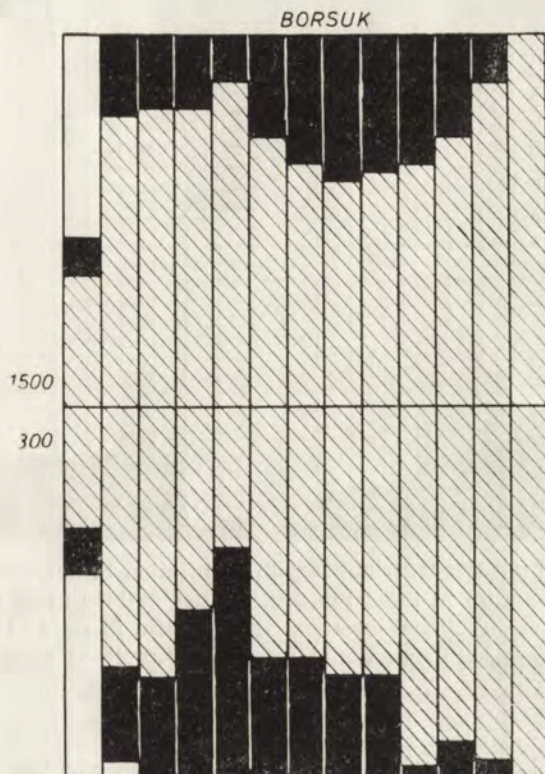


Fig. 2. Formation of the left leg-right leg differentiation to non-directional cues. Denotations as in Fig. 1. Columns below the middle line denote tone 300 cps trials, columns above the middle line denote tone 1500 cps trials. Note that the passive movement trials are here much less abundant than in Fig. 1

Variety 3 (L-B differentiation). In three dogs the right leg-left leg differentiation was established to the lightening of a lamp and the sound of a buzzer, both operating from the front of the animal. The task of differentiation turned out to be as easy as that with directional cues and the dogs mastered in less than 400 trials (see Table I).

Part II

Since in three of our dogs subjected to tone differentiation this task was ultimately solved, it was decided to bring the frequencies of tones nearer and nearer to one other to see how this procedure would affect

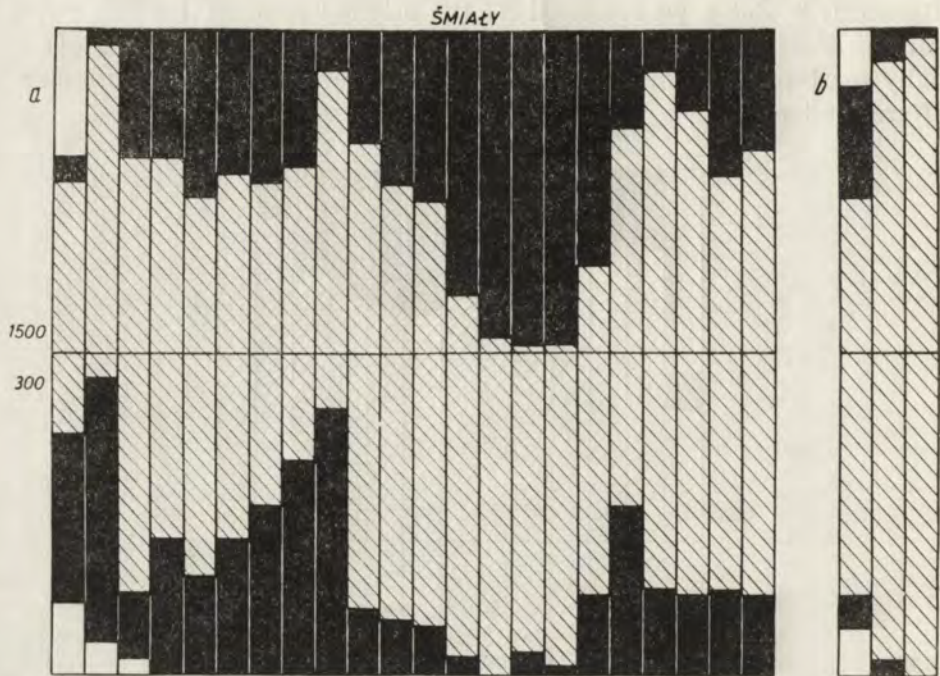


Fig. 3. Formation of the left leg-right leg differentiation to non-directional cues (a) and to directional cues (b) in the same dog. All denotations as in Fig. 2. Note that the training with non-directional cues was unsuccessful in spite of 1760 trials whereas the training with directional cues was completed after 160 trials

the performance of the animals. In three new dogs the go-no go differentiation was established to tones of 1500 c/sec and 300 c/sec respectively, and thereafter exactly the same gradual approximation of the tones was carried out. If the performance of the dogs was errorless, six experimental sessions were given (about 50 trials) and then the next step of approximation of tones was made. If the animals did perform errors the experiments with a given pair of tones lasted until the performance reached a criterion of 80% of correct responses in that series.

The results of the experiments in both groups are represented in Table II. Each figure of the table represents the percentage of correct responses in the last six sessions of a given task (including six last sessions of the original training).

It may be seen that in experiments with go-no go differentiation the gradual approximating of the tones produced only a negligible number of wrong responses, consisting in performing the trained movement in negative trials. In general, however, the performance of all three animals was errorless.

Table II

The effects of gradual approximation of differentiated tones upon the performance of animals

The frequencies of tones

Dogs	1500-300	1400-400	1300-500	1200-600	1100-700	1000-800
Left leg-right leg differentiation						
Fifek	97	83	88	80	79	79
Zabot	98	93	98	87	80	77
Borsuk	97	85	92	89	97	87
Average	97	87	93	85	85	81
Go-no go differentiation						
Bil	100	100	100	98	96	100
Kłapouch	97	100	100	100	100	100
Nicpoń	100	100	100	100	100	93
Average	99	100	100	99	99	98

The results in animals with go left-go right differentiation were quite different. In none of the dogs was the errorless performance attained, and the animals did not display any tendency to improve their responses during the training. In average the performance in all the dogs did not surpass 90% and became slightly worse as the difference between the tones decreased. One of the dogs (Borsuk) displayed a severe neurosis in the 1000 c/sec versus 800 c/sec differentiation, and had to be „cured” by return to the original 1500 c/sec versus 300 c/sec differentiation.

DISCUSSION

The aim of this paper was to examine the course of right leg-left leg differentiation when two auditory CSs were operating from the same place. It has been found that whereas differentiation between the auditory and visual stimuli did not present any difficulties, the differentiation between two auditory stimuli was exceedingly difficult and in some dogs could not be mastered at all. This was true both with regard to quite distinct stimuli such as metronome and buzzer and with regard to two tones widely remote from one another (1500 cps versus 300 cps).

These results clearly support the thesis that the qualitative aspects of the CSs are of no value for the dogs in the left leg-right leg differentiation of auditory stimuli, and these dogs base their responses chiefly, or exclusively, on orienting reactions elicited by the presented stimuli.

The easiness of differentiation between light and sound is easily explained by admitting that the visual and auditory stimuli obviously elicit quite different patterns of orienting responses.

It was further found that if the training of the left leg-right leg differentiation to the two auditory stimuli is persistent, it is possible, at least in some dogs, to attain the errorless performance. Therefore, the problem arose whether the animals are able eventually to utilize the qualitative cues in this type of differentiation, or whether they still make profit of the proprioception of orienting reactions, which is supposed to be slightly different to metronome and bubbling, or to tones of high and low pitch. In order to answer this very question the approximation of differentiated tones was undertaken.

The results of these experiments seem to suggest that rather the second hypothesis is true. It may be supposed that if the animals learned to utilize the qualitative cues for left leg-right leg differentiation, they would be able to cope with the gradual approximation of tones in the same way as in the go-no go differentiation. It has been shown in our experiments that the latter task does not present any difficulty for the dogs and their responses to the gradually approximating tones are practically errorless. On the other hand, the approximation of the tones in the left leg-right leg differentiation took another course, since the animals were not able to solve completely the problem and their errors slightly increased with the decrease of the difference between the tones.

In an earlier paper of one of the authors (Konorski 1962, see also Konorski 1967) the distinction was made between the process of discrimination, i.e. learning to discriminate two stimulus-patterns on the perceptual level and the process of differentiation in which the discrimination of the two stimuli is utilized for learning to perform a different response to each of them. It is clear that with regard to the qualitative aspects of a metronome and bubbling, or a tone 1500 cps and a tone 300 cps, the discrimination of the stimuli is perfect even before differentiation training. In consequence, in the go-no go training, in which these very aspects are utilized, the animal must merely learn which of the two different stimuli signals food and which one signals no-food. This is why the process of differentiation is very easy. On the other hand, since in the go left-go right differentiation this cue cannot be utilized because of the lack in the animal's brain of the appropriate potential connections (Ławicka 1964, Dobrzecka and Konorski 1967, Konorski 1967) the animal must resort to another cue, namely that of proprioception of orienting responses. It may be supposed that if both stimuli are presented from the same place, the corresponding proprioceptive stimuli are originally not discriminated by the animals, and that they learn to do so in the

course of differentiation training. This is why this training is so prolonged and why during a long period it seems to be hopeless.

It is interesting to analyse the strategy adopted by some dogs in the first stage of training. Since the task of left leg-right leg differentiation is in that stage insoluble (because of the lack of discrimination of the two proprioceptive cues), the animals tend to perform the same response to both stimuli. But it appears that the response is rewarded by food only to one stimulus and not to the other. Since the qualitative difference between the stimuli is clear for the animal, he learns to perform the trained movement to one of the stimuli and abstain to perform it to the other one, according to the go-no go procedure.

In other cases the animals learn, in the first period of training, to perform the same movement to both stimuli, accepting willy-nilly the irregular schedule of reinforcement. Only when the dogs begin to discriminate between the two proprioceptive cues connected with each of the two stimuli, do they learn to perform both movements, making at first some errors and then improving their performance.

SUMMARY

1. The left leg-right leg differentiation in dogs to two considerably different auditory stimuli, sounding from the same place, is a very difficult task which can be mastered only after more than a thousand trials. On the contrary, the same differentiation to an auditory and visual CS is very easy.

2. After the left leg-right leg differentiation to two widely separated tones has been established, the gradual approximation of these tones leads to the substantial increase of incorrect responses.

3. It is supposed that the left leg-right leg differentiation is based only on the difference between the orienting responses produced by each of the CSs, but not on their qualitative properties.

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THE EFFECT OF AMYGDALOID STIMULATION
ON DAILY FOOD INTAKE IN CATS

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In the studies on nervous control of food intake, relatively little attention has so far been paid to the effect of amygdaloid stimulation on daily consumption. In their chronic experiments on cats, Fonberg and Delgado (1961) obtained some decrease in daily intake following electrical stimulation of the basolateral part of amygdala. Grossman and Grossman (1963) were interested in the effect of electrical stimulation on both food and water ingestion in the rat. They distinguished in the ventral amygdala two critical areas, a posterior one which inhibited both the food and water intake and an anterior area, which inhibited feeding but facilitated drinking. Stimulating the ventral part of the amygdala with adrenergic and cholinergic agents, Grossman (1964) obtained respectively an increase in the amount of food and water ingested. Both the electrical and chemical stimulation were effective only when the animals were hungry and thirsty.

The facilitation of food responses in satiated animals has also been observed during the electrical stimulation of the amygdala (Robinson and Mishkin 1962). According to Gastaut (1952), after amygdaloid stimulation food was eaten avidly. The authors referred to above did not, however, deal with the effect of chronic stimulation of these alimentary positive points on the daily food intake and did not localize them.

It results from our previous studies that the area facilitating the food responses in cat is situated in the anteromedial part of the amygdaloid complex. This has been shown by lesions of this part which resulted in hypodipsia and hypophagia with a particular aversion towards raw

meat (Lewińska 1967) and, in the case when electrical stimulation has been applied, in an increase in the conditioned food reaction (Lewińska 1968). The inhibiting area has mostly been localized in the region of the basal parvocellular nucleus except for its medial part adjacent to the cortico-medial nuclei. The aim of the present work was to establish whether or not electrical stimulation of these inhibiting and facilitating areas exerts its effect also on the daily solid food and milk intake in cat.

MATERIAL AND METHOD

Experiments were performed on 26 adult cats of both sexes. The animals were fed ad libitum with milk and a mixture of boiled cereal and horse meat (at a ratio of 1 kg of cereal to 0.5 kg of meat). In addition, they were fed with 60 g of raw horse meat daily. The daily food intake was measured and recorded for about 6 weeks before and 6—8 weeks after the surgery.

The operation was performed under Nembutal anesthesia (40 mg/kg). Monopolar electrodes were implanted according to a slightly modified version of Delgado's method (1955) and with the use of the Jasper and Ajmone-Marsan atlas (1954). A detailed description of the procedure of implantation has been given in one of the previous papers (Lewińska and Romaniuk 1966). Four electrodes were introduced symmetrically into the cerebrum, two in each hemisphere. The implantation was performed in four groups of animals. In the first group, electrodes were implanted in the posterior, in the second group, in the middle and, in the third group, in the anterior part of the basal parvocellular nucleus (Abp), and in the anterior amygdaloid area (Aa). In the fourth group, electrodes were implanted in the cortico-medial nuclei (Aco and Am). Since the results obtained in the second and third groups were not uniform, groups IIA and IIIA were distinguished.

The stimulation of the amygdala was started within about two weeks after surgery. For four weeks, every other day, the amygdala was stimulated about 15 times during each experimental session which, on the average, lasted 30 min. During the time of stimulation the raw meat was available. Irregular intervals (30 sec to 3 min) were applied between individual stimulations which persisted for 5 to 15 sec. Rectangular impulses (50 c/sec, 1 msec, 0.1—0.5 ma) were used as stimuli.

After completing an experimental series, the points under study were coagulated for 15 sec with a 3 ma current. After a lapse of about a month, cats were sacrificed and their brains perfused with 10% formalin. Paraffin sections 20 μ thick were sectioned in the frontal plane. Every tenth of them was stained by means of Nissl's method.

RESULTS

Inhibitory effects

Group I. Electrodes were implanted in the posterior part of Abp, between frontal planes 9.0 and 11.0, in five cats.

In two cats the implantation itself completely inhibited for a few days solid food and milk intake. On the third day, one of these two cats,

started to drink milk and, on the fifth day, to eat solid food. The other cat neither ate nor drank for four days. During the period of two weeks which preceded electrical stimulation, a pronounced decrease was recorded in the milk intake in all cats and in the amount of cereal ingested by two of them. This, for the entire group of five cats, was on the average expressed respectively in a 49% and 14% decrease. During the period of stimulation a further drop was recorded in the food intake. A decrease in the consumption of cereal was observed also in those cats in which no changes after inserting of electrodes appeared. On the average, during the four-week period of stimulation, the daily intake of milk decreased, as compared with corresponding presurgery values, by 71% and that of cereal by 51% (Fig. 1, Group I and Fig. 2).

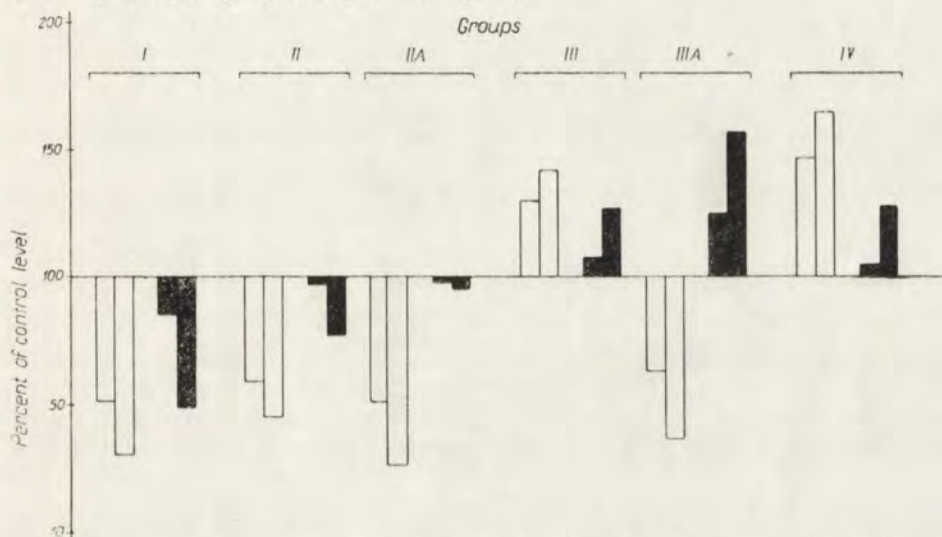


Fig. 1. Changes in average daily intake of milk (white bars) and cooked cereal-meat (black bars) in cats with implanted electrodes. The results are expressed as a percentage of the preoperative value. The first bar of each pairs depicts irritating effect of implanted electrodes (average data over two weeks). The second bar illustrates the effect of electrical stimulation (over four weeks). Localization of electrodes: Group I, posterior part of Abp; Group II, medial part of Abp; Group IIA, central part of Abp and medial part of Al; Group III, area of Aco, Am and adjacent Abp; Group IIIA, area of Aco and central part of Abp; Group IV, anterior part of Abp and adjacent dorsal part of Aa

In three cats, the implantation of electrodes decreased the appetite for raw meat. One of them refused meat for 10 days. During the period of stimulation, the raw meat intake was strongly reduced in all cats.

During the 6 — week postoperative period, in all cats the body weight decreased by an average of 11%.

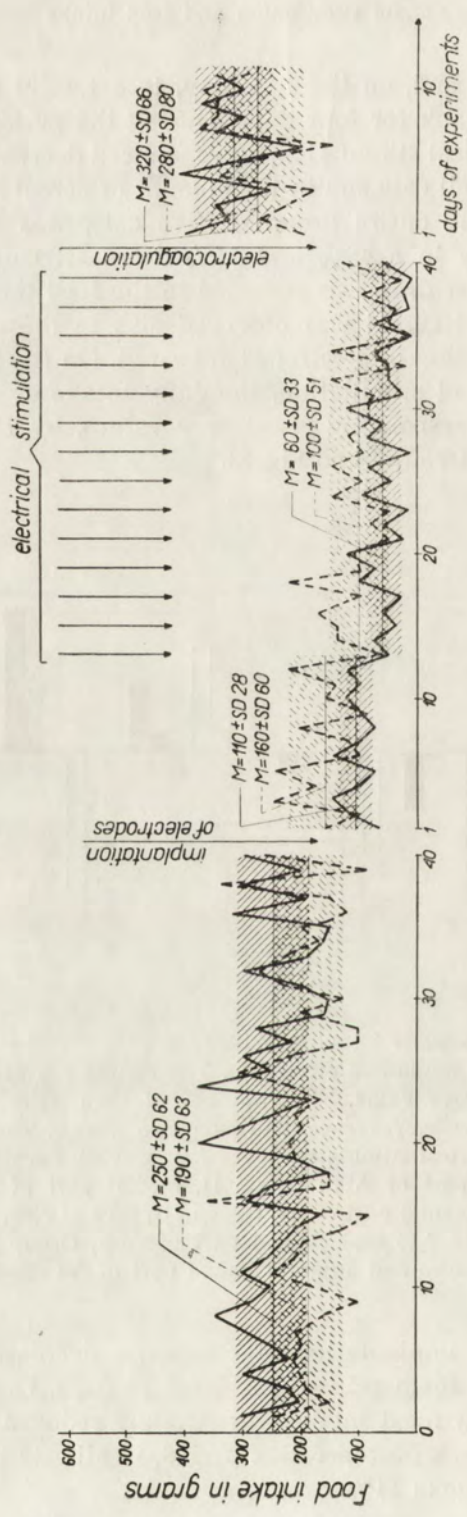


Fig. 2. Daily intake of milk (continuous line) and cooked cereal-meat (dashes) in a typical cat of Group I with electrodes implanted in the posterior part of Abp. The shaded areas represent standard deviations

Group II. Electrodes were implanted in the medial part of Aby, between frontal planes 11.0 and 13.0, in five cats.

In this group of animals the results were very similar to those recorded in Group I. The only difference consisted in the fact that within two weeks after the implantation of electrodes, the consumption of cereal was almost completely unchanged whereas the milk intake, comparable to that of Group I, decreased on the average by 41%. During the period of stimulation, the ingestion of cereal dropped, as compared to the pre-surgery level, by 23% and that of milk by 55% (Fig. 1, Group II).

Group IIA. In this group, consisted of five cats, some electrodes were implanted in the central part of Abp and some in the medial part of Al (lateral nucleus), between frontal planes 10.0 and 13.0.

No essential influence was exerted on the consumption of cereal by either the implantation of electrodes, or stimulation. On the other hand, considerable changes were observed in the milk intake, which during the period prior to electrical stimulation dropped, on the average, by 49% and, during period of stimulation, by 74% (Fig. 1, Group IIA). At the same time, a decrease in the appetite for raw meat was recorded in three cats.

During the postoperative period, the body weight of the animals of Group II and IIA decreased on the average by 7%.

In most cats belonging to groups mentioned above, a general mobility was decreased both by the inserting of electrodes and by electrical stimulation. It was usually found that stimulation arrested eating and, depending on intensity, evoked attention, sniffing, vomitive movements, licking, gnawing and in some cases several motor and autonomic responses. With repeated stimulation, the successive inhibition became longer and longer, sometimes persisting for several hours. Some cats of Group IIA displayed an increased timidity.

After coagulation of the points under study, the feeding behavior of the animals changed. Cats started to eat their entire daily doses of meat and increased their consumption of milk and cereal. The measurements of the daily food intake were continued for two weeks in three cats (Fig. 2).

Facilitatory effects

Group III. Electrodes were implanted in Aco and Am between frontal planes 11.5 and 13.0, in three cats.

As shown in the illustration (Fig. 1, Group III and Fig. 3), both the milk and cereal intake increased in the postoperative period. Within two weeks after the implantation of electrodes, ingestion of milk increased on the average by 28% and that of cereal only by 9%, whereas during

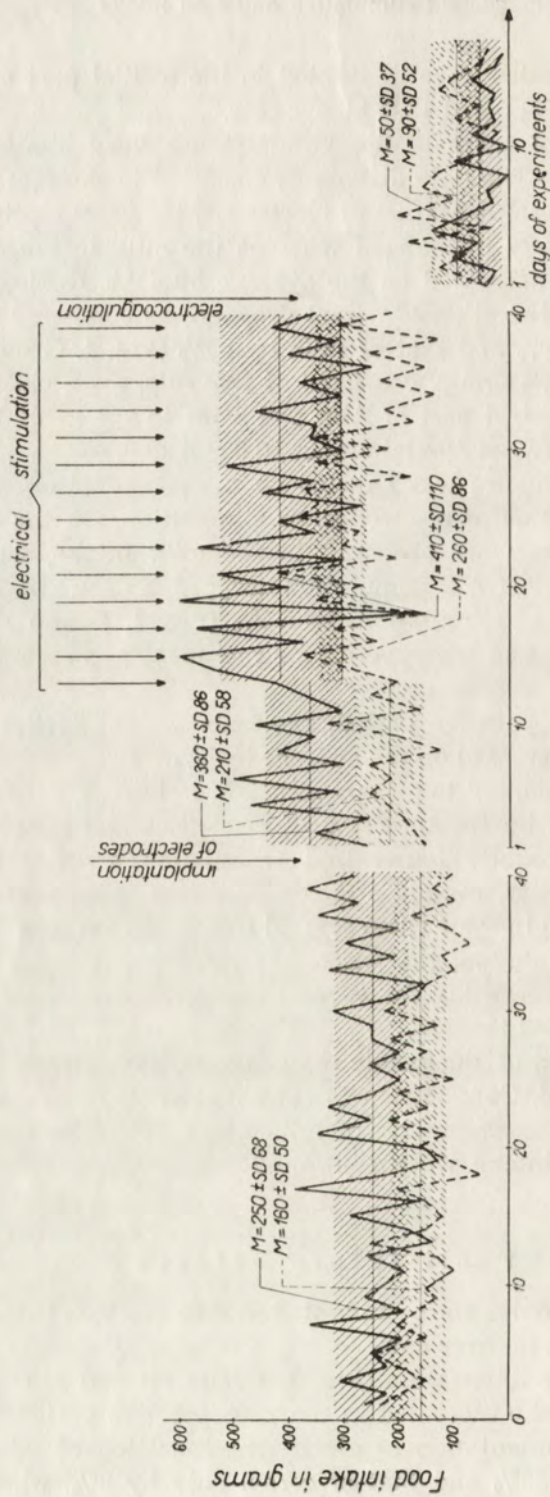


Fig. 3. Daily intake of milk (continuous line) and cooked cereal-meat (dashes) in a typical cat of Group III with electrodes implanted on the boundary of Aco, Am and Abp. The shaded areas represent standard deviations

the electrical stimulation corresponding figures exceeded the preoperative level by 42% and 25% respectively. Within about four weeks after surgery, the milk and cereal intake started to decrease. In two cats, it dropped below the preoperative level. The last-named results was not changed by either stimulation or coagulation applied thereafter.

Group IIIA. Two electrodes were implanted in each of three cats in cortico-medial nuclei and two in the central part of Abp. In these cats, the milk intake diminished by 38% during a two-week period preceding electrical stimulation and by 55% during the period of stimulation, whereas the ingestion of cereal increased at first by 25% and afterwards, that is, during the period of stimulation, by 57% (Fig. 1, Group IIIA).

Group IV. In five cats of this group, electrodes were implanted in the anterior part of Abp and mostly in the dorsal part of Aa, between frontal planes 13.0 and 15.0.

In one cat, the implantation and stimulation elevated only the milk intake, whereas a slight drop was recorded in the ingestion of cereal. Another cat displayed some increase in the consumption of milk, which was observed only for a week following surgery and afterwards both the milk and cereal intake dropped pronouncedly below the preoperative level. This effect was not changed by electrical stimulation and the coagulation evoked a further drop in consumption.

In the remaining three cats, the implantation of electrodes affected primarily milk intake which was enhanced on the average by 47%. During the period of stimulation, the consumption of milk was elevated by 65% as compared with the preoperative period and that of cereal by 28% (Fig. 1, Group IV). In these cats, electrodes were implanted between frontal planes 14.0 and 15.0.

Some cats of Group III and IV manifested a pronounced appetite for raw meat. One cat of Group III behaved aggressively when attempts were made to take the meat away. Stimulation either remained without effect on general behavior of animals, or evoked agility, sniffing, searching and evident symptoms of voracity. The response of anger obtained from some points was manifested by growling and striking with the tail against the floor. During the period of hyperphagia, the body weight of cats increased on the average by 10%.

DISCUSSION

The drop in the daily consumption of solid food and milk was obtained by stimulation of the most part of the Abp area. The stimulation of the anteromedial area of amygdala resulted in a quite opposite effect, that is, an increase in the intake of both kinds of food. The changes observed

concerned to a different degree the ingestion of milk, raw meat and cereal. The stimulation of Abp, determined as an inhibitory area (Lewińska 1967), evoked usually a pronounced aversion towards raw meat and milk, whereas the stimulation of the area, determined as a facilitatory one, conspicuously increased the milk intake. Since raw meat was not fed *ad libitum*, the increase in the appetite for this kind of food could not be quantitatively estimated. As the lesions of the regions under study resulted in most cases in a greater aversion towards meat than towards cereal (Lewińska 1967), we may only presume that the consumption of raw meat would reach a much higher level. The results obtained indicate, therefore, that the most intensive changes involved the attitude of cats towards those kinds of food which, under normal conditions, were the most attractive to them (milk and raw meat). Moreover, what is particularly striking is a great sensitivity of the neuronal elements related to the control of the intake of these kinds of food. It was only the implantation of electrodes itself which exerted such a strongly irritating effect, increasing or decreasing the appetite, so that it could not be subsequently intensified to any great extent by a sporadic electrical stimulation.

Grossman (1964) presumes that in view of the very low seizure threshold of the amygdala, it is quite possible, that electrical stimulation may produce electrophysiological changes which render the surrounding tissue inactive and thus produce a temporary functional lesion rather than excitation. The assumption that the implantation of electrodes during our experiments might cause functional lesions is testified against by the fact, that electrical stimulation produced changes identical in character with those caused by the insertion of electrodes and, that coagulation reverted the effect of stimulation, that is, an increase in the consumption was obtained instead of decrease and vice versa. In two cases, however, neurons were damaged soon after the implantation of electrodes and, in two others, after a lapse of two weeks during the period of electrical stimulation.

In a few cases mixed results were obtained, that is, a change occurred in the ingestion of one only kind of food (solid food or milk), or an increase was recorded in the intake of one kind and a decrease in the intake of the other kind of food. The histological analysis has shown that in such cats electrodes were situated either on the boundary of the areas which were determined as inhibitory and facilitatory, or some electrodes were situated in the former of these areas and another in the latter. It can be also supposed that facilitatory as well as inhibitory regions are topographically differentiated having representative areas for specific

foods. The results obtained up to the present time do not allow for more exact localization of these areas, it seems however that they exist.

In the case of our experiments during which cats were not offered water, the consumption of milk depicted, at the same time, the demand for water. Our observations coincide to a considerable extent with those of Grossman (1963) who, stimulating the anterior part of amygdala in rats, obtained an increase and, stimulating the posterior part, a decrease in the water intake. Some drop in daily food intake as a result of chronic stimulation of basolateral part of amygdala in cats reported earlier by Fonberg and Delgado (1961) agrees also with our results.

Because of lack of wider research material concerning the influence of chronic stimulation of various parts of amygdala on the food consumption it would be interesting to compare our results to similar studies carried out on hypothalamic alimentary centers. In contrast to amygdala results the effect of chronic stimulation of the hypothalamic satiety center located in the ventromedial nucleus on the daily food intake has not been clearly shown. The effect of the stimulation of ventromedial nucleus on the animals' behavior was also different: no symptoms have ever been obtained of aversion towards food which occur often during the stimulation of the amygdala and, according to Robinson (1964), ejection of the food from the mouth occurred less frequently than the food intake. Similar results were obtained during our experiments on cats (Lewińska 1967a) and, moreover, we found, that the inhibitory threshold of the alimentary reactions mostly coincided with the threshold of the reaction of aggression or of fear (Lewińska and Romaniuk 1966).

With regard to works devoted to the increase in the food intake as an effect of the stimulation of the hypothalamic „feeding center” located in the lateral part of hypothalamus, individual authors differ from one another in methods used and in their presentation of the dynamics evoked by hyperphagia. Delgado and Anand (1953) maintain, that hyperphagia in cats developed gradually beginning with the second day of stimulation and reaching a value of about 700%. In contrary to the results we obtained from the amygdala, a larger inertia was observed in the consumption of milk which started to increase only after a few days. In Steinbaum and Miller's (1965) experiments, rats began to overeat after 8 days from stimulation and after 19 days demonstrated very marked hyperphagia. Between stimulations the animals ate significantly less than control animals. According to Delgado and Anand (1953) after stopping the stimulation the ingestion of meat returned in cats abruptly to normal level.

Our experiments on amygdala differ, therefore, from those performed on the hypothalamus. We did not investigate the problem how the food intake is distributed over the entire 24 hr period. However we noticed

that the daily consumption of both milk and cereal was changed despite the fact that this was the food offered after electrical stimulation. On the other hand, in the light of the results obtained, the irritative effect of electrodes, inserted in the brain, may be considered as permanent. It is possible, that the results were dependent upon irritative foci set up by the presence of metal electrodes in the brain.

SUMMARY

Electrodes were implanted into the ventromedial part of amygdala in 26 cats. Two weeks after the implantation during a period of about a month, this region of amygdala was stimulated every other day for about 30 min.

Changes in the daily milk intake reaching about 40% of the control value, were observed as an effect of an irritating action of the electrodes themselves. As a result of the electrical stimulation, these changes were additionally intensified by about 20%. The effect of the irritating action of the implanted electrodes on the ingestion of cereal was less intensive. Changes of the order of about 50% occurred only during the electrical stimulation.

A decrease in the daily intake of milk and cereal occurred in cats with electrodes implanted in basal parvocellular nucleus. In most of these cats, a simultaneous strong aversion towards raw meat was observed. An increase in the daily consumption of milk and cereal occurred in cats with electrodes situated in the anteromedial area (area amygdaloid anterior, anterior and medial part of basal parvocellular nucleus, medial and cortical nuclei). Some of these cats displayed an increased appetite for raw meat.

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CORTICO-HYPOTHALAMIC INTERACTION IN CATS¹

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It is well known that many functions are regulated by both cortex and hypothalamus (Hess 1948, Anand 1959, Encabo and Ruarte 1964, Stuart et al. 1964, Chernigorskii 1965, Santibañez-H. et al. 1965, Stutinsky and Guerne 1965ab). In the present paper an analysis of the direct influence of the cortex on the hypothalamus was undertaken. As an indicator of hypothalamic function, evoked potentials to different sensory modalities were utilized (Dell 1952, Ingvar and Hunter 1955, Feldman et al. 1959, Romaniuk 1965).

METHODS

The subjects were 20 cats whose weights were 2.5 to 3.8 kg. The experiments were performed under 80 mg/kg chloralose anesthesia. The animals were tracheotomized and the femoral vein was cannulated. Trepanation was carried out after the head had been placed in a stereotaxic apparatus, and in order to preserve the cortex in a good functional state such procedures as successive small trepanations, placing agar-agar on the cortex, covering exposed cortex with pieces of soft plastic material, etc. were employed singly or in combination. Resection of the nictitating membranes and suturing the eyelid to the skin surrounding the eye were carried out in order to facilitate stimulation of the visual receptor.

Bipolar nichrone electrodes, 0.3 mm wide, were used to record from the hypothalamus. To stimulate the cortex, two independent silver or platinum wires, 2 or

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3 mm apart, were used. In cortical recording a silver bipolar electrode was used, separated by 0.5 mm at the poles.

Somatic stimulation was effected by a square pulse (0.3 msec duration, 4–6 v) applied directly to the radial nerve and auditory stimulation by an amplifying system to a loudspeaker. The visual stimulus was a flash of 30 msec duration produced by a neon lamp (type NE-2H) placed before the eyes. All stimulations were monitored by a Grass stimulator. The hypothalamus was stimulated by single square pulses (0.5 msec and 2–6 v) and to stimulate the cortex a train of 3 square pulses (0.1 msec duration, 300 c/sec frequency and 4–6 v) were applied.

When the effect of cortical stimulation was tested on exteroceptive evoked hypothalamic activity, a constant delay of 50 msec was maintained between conditioning and test stimuli. In order to avoid depression or fatigue, the preparation was stimulated at a very slow rate (one stimulus every other 6 sec). Recording was done by oscilloscopes and polygraph equipment.

At the end of each experiment the animal was perfused. The brains were fixed and processed histologically.

RESULTS

Different points of the hypothalamus were selected to study their reaction to cortical stimulation. Observation was especially centered on the behavior of the dorsal hypothalamic area.

Effect of cortical blocking on exteroceptive hypothalamic activity. Several experiments were carried out in order to clarify if local depression of the cerebral cortex is able to alter the exteroceptive activity of the hypothalamus. Filter paper (0.5 cm²) soaked in a solution of Nembutal (15 mg×cc) was placed on the sygmoidean gyrus, lateral gyrus, or suprasylvian gyrus of the ipsilateral cerebral cortex. When visual, tactile or auditory evoked responses of the cortex were absent, the exteroceptive potentials of the hypothalamus were seriously affected. For example see Fig. 1. The diminution of hypothalamic evoked potentials elicited by stimulation of the ipsilateral radial nerve is shown. If both sides were blocked, the effect was greater. This effect was reversible: 15 min after withdrawing the filter paper the hypothalamic evoked activity to auditory, visual or tactile stimulation reappeared unimpaired.

Control experiments showed, however, that small doses of Nembutal injected intravenously (4–6 mg×kg) also blocked the exteroceptive activity of the hypothalamus (in some instances, a small positive deflection would remain).

Therefore, the effect of mechanical spreading depression (which abolishes cortical evoked potentials) on hypothalamic activity was also tested. Fig. 2 shows the effect of such cortical spreading depression on hypothalamic activity produced by radial nerve stimulation. The electrical sti-

mulation of the depressed cortical zone did not induce an inhibition of hypothalamic activity (see next Section). Recuperation followed after 25—30 sec. The visual evoked potentials were the most sensitive to this blocking manipulation, while the responses to the radial nerve were the smallest.

It was observed that on some occasions exteroceptive activity suddenly started to decrease in amplitude until it was not visible any more. At

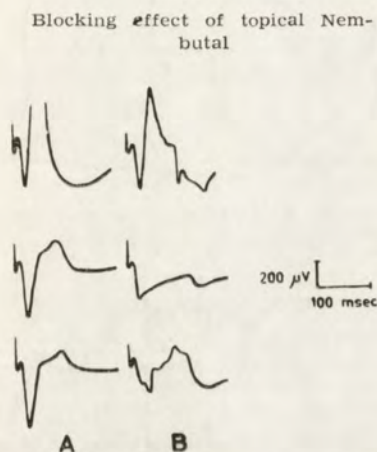


Fig. 1. Cat under chloralose. Recording electrode placed into dorsal hypothalamic area. A, Hypothalamic evoked potentials by electrical stimulation of the ipsilateral radial nerve. B, 5 min after a 0.5 cm² filter paper soaked in 15 mg × cc Nembutal solution was placed into the ipsilateral anterior sigoidean gyrus. Note the modification in amplitude shown by the evoked potentials

Blocking by spreading depression

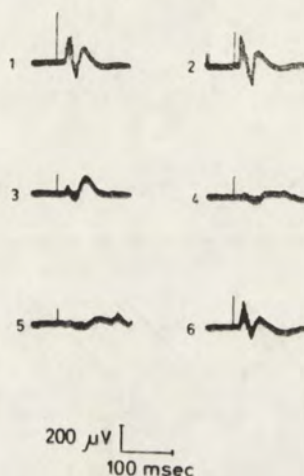


Fig. 2. Cat under chloralose. Recording electrode placed into the dorsal hypothalamic area. 1, Evoked potential elicited by electrical stimulation of the ipsilateral radial nerve. 2, Cortical conditioning stimulation was ineffective. 3—5, Spreading depression, induced mechanically, inhibited evoked activity. 6, Return to control after 25 sec

the beginning, this phenomenon was inexplicable, but later we realized that it was connected with cortical pallor or other cortical vascular accidents.

In short, manipulation of blocking the excitability of the cerebral cortex induced a reduction of size of the exteroceptive evoked potentials of the hypothalamus. This reduction particularly affected the second negative wave which was completely blocked, greatly diminished the positive wave, and made the first negative wave, if present, disappear.

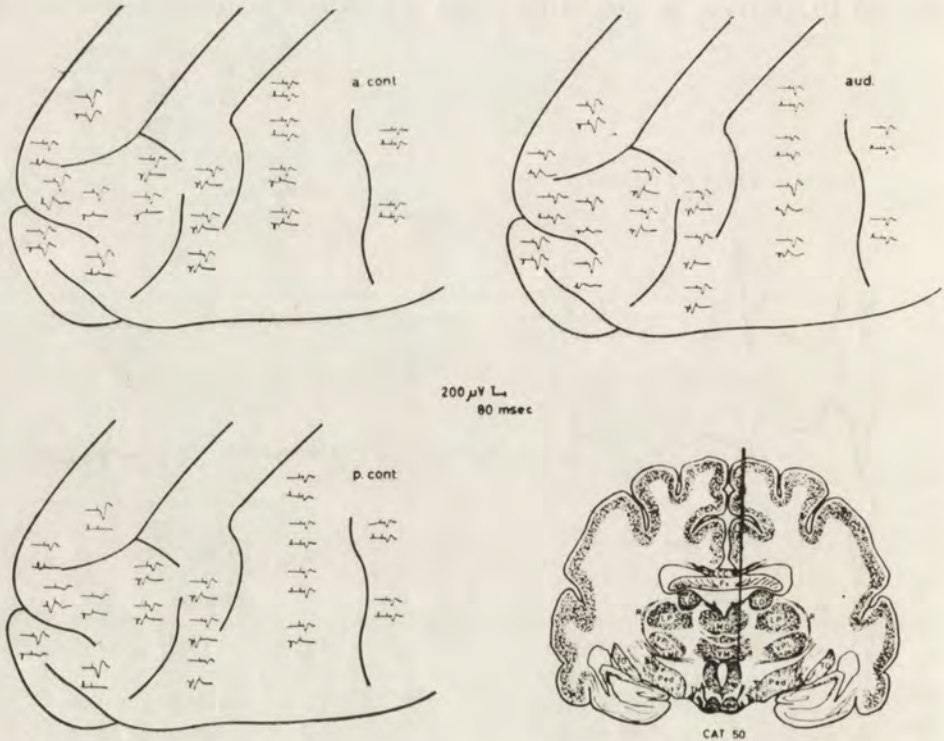


Fig. 3. Cat under chloralose. The position of the recording electrode is indicated. Double stimulation technique was used. Each cortical point tested presents two oscilloscopic records. Upper trace: hypothalamic response to a given sensory modality (aud., auditory stimulation; a. cont., electrical stimulation of the anterior contralateral radial nerve; p. cont., electrical stimulation of the posterior contralateral sciatic nerve). Lower trace: same, but preceded by an electrical shock given at the indicated point 50 msec before

Effect of cortical stimulation on exteroceptive hypothalamic evoked potentials. The external surface of the cerebral cortex was systematically mapped to observe the effect of its electrical stimulation on hypothalamic evoked potentials provoked by radial nerve stimulation, flashes and clicks. Three types of cortical points could be distinguished: (i) some points

evoked a potential in the hypothalamus and, at the same time, prevented the appearance of exteroceptive evoked potentials; (ii) other points did not evoke a response but prevented, totally or partially the hypothalamic exteroceptive activity; (iii) and some others, in which the same stimulation parameters were used, were ineffective (Fig. 3 and 4).

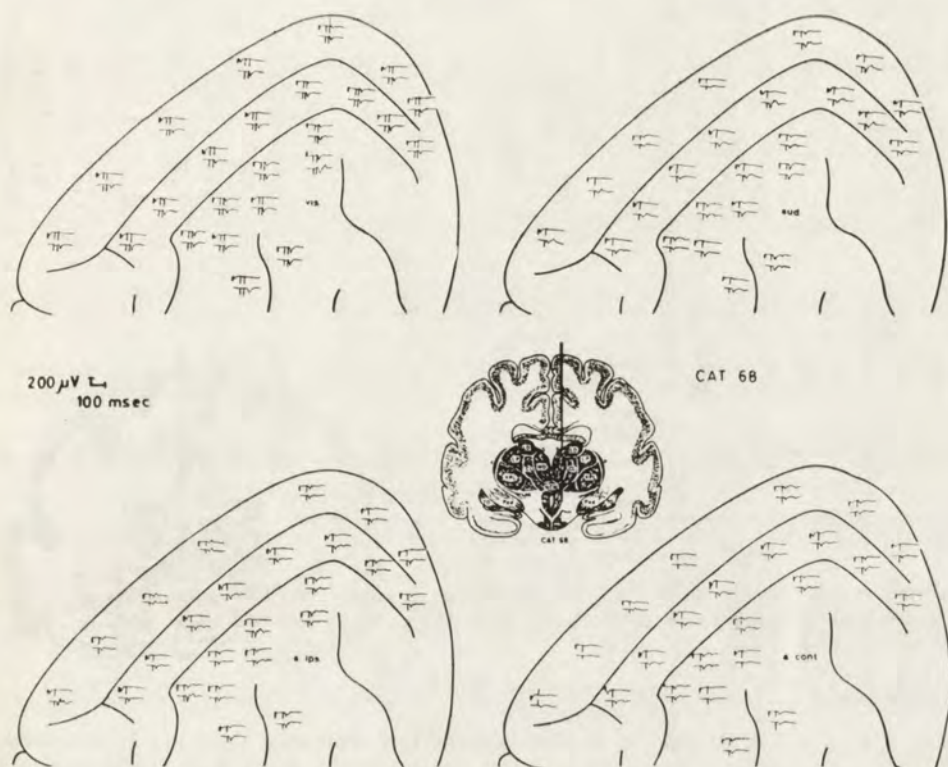


Fig. 4. Cat under chloralose. The position of the recording electrode is indicated. Double stimulation technique was used. Each cortical point tested presents two oscilloscopic records. Lower trace: the hypothalamic response to auditory stimulus (aud.), visual stimulus (vis.) and electrical stimulation of the anterior contralateral radial nerve (a.cont.). Upper trace: same, but preceded by a shock at the indicated point given 50 msec before

The hypothalamic evoked potentials induced by cortical stimulation were generally biphasic, positive-negative. The latency to the positive peak was around 16–25 msec, and the total duration of the event was around 30–60 msec. The cortical zones from which this activity was elicited were concentrated in the following areas: sigmoidean gyrus,

posterior part of the lateral gyrus and suprasylvian gyrus (Fig. 3, 4 and 5). Other cortical points had only an inhibitory effect on the hypothalamic exteroceptive evoked potentials, without inducing evoked activity.

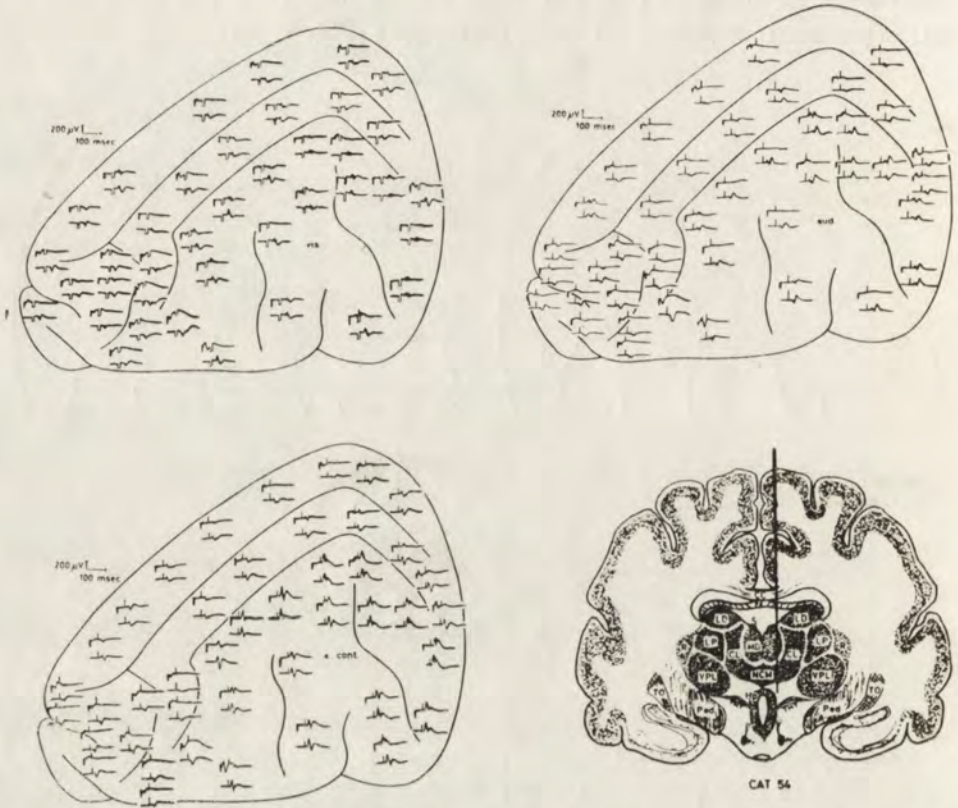


Fig. 5. Cat under chloralose. The position of the recording electrode is indicated. Double stimulation technique was used. Each cortical point tested presents two oscilloscopic records. Lower trace: hypothalamic response to auditory stimulus (aud.); visual stimulus (vis.); electrical stimulation of the anterior contralateral (a.cont.) and anterior ipsilateral (a.ips.) radial nerve. Upper trace: same but preceded by a shock given 50 msec before, at the indicated cortical point

DISCUSSION

In spite of the fact that exteroceptive evoked potentials in the hypothalamus have long been observed by different authors (Dell 1952, Ingvar and Hunter 1955, Feldman et al. 1959, Abrahams et al. 1962, Feldman 1963, Malliani et al. 1965, Romaniuk 1965, Rudomin et al. 1965) and even single unit activity has been analyzed (Cross and Green 1959, Cross and Silver 1963, Koizumi et al. 1964, Stuart et al. 1964, Dafny et al. 1965,

Rudomin et al. 1965ab, Ishikawa et al. 1966) very little is known about their functional significance. Some studies have shown that the evoked potentials are abolished by electrical activation of the mesencephalic reticular formation (Feldman et al. 1959) but the fact that the latency of the hypothalamic and reticular potentials are comparable (Rudomin et al. 1965) rules out the possibility that the information arriving at the hypothalamus is relayed at the reticular level. Another effect related to the reticular formation is that a lesion of this structure reduces or abolishes the long latency evoked potential recorded in the ventromedial hypothalamic nucleus and not the short latency one recorded in the posterolateral hypothalamus (Feldman 1963). Our results showed that electrical stimulation of the cortex blocks hypothalamic activity either producing an evoked potential or merely blocking without any other manifestation in the hypothalamus. This seems to confirm the observation of Niemer and Jimenez-Castellano (1950) suggesting, on the basis of neuronographic methods, the existence of functional connections between the cortex and the hypothalamus. Nevertheless it is necessary to point out that cortical blocking, either through drugs, or by mechanical depression, induced an inhibition of exteroceptive hypothalamic activity. In the case of drugs it may be objected that they are incorporated into general circulation and act directly on the hypothalamus (Feldman et al. 1959, Abrahams et al. 1962) but this possibility is ruled out with the spreading depression technique. In the case of the cat, the cortico-hypothalamic connections seem to be polysynaptic because of the delay of the response. Lundberg (1960) showed that there is no demonstrable cortico-hypothalamic connection in rabbits. Auer (1956) proved that the frontal cortex in cat is connected with ventromedial, mammillary and posterior nuclei. Other authors have found connections in monkeys and human beings (Ward and Culloch 1947, Clark et al. 1950, Nauta 1950, Beck et al. 1951, Adey and Meyer 1952, Ban 1965) but it is not easy to say if such connections are responsible for our findings.

Even if it seems contradictory, the stimulation of certain cortical points and the functional depression of the cortex lead to the same results. This contradiction, nevertheless, is only apparent because punctiform stimulation activates given synaptic pathways, while spreading depression or topical Nembutal affect the cortex in its totality, producing a massive disruption of its inhibitory-excitatory influence on subcortical structures. There are many instances in which the cortex or other telencephalic structures modulate diencephalic nuclei. Meulders et al. (1963) observed that decortication facilitates the activity of the centrum medianum, Meshcherskii and Guston (1964) observed that spreading depression inhibited visual activity of the lateral geniculated body and Meshcherskii et al.

(1963) showed that strychnization of the visual cortex facilitates its activity. Krauthamer and Feltz (1965) observed that units belonging to the CM are inhibited by electrical stimulation of the nucleus caudatus.

If the classic observation of Bard (1928) and that of Abrahams et al. (1962) is accepted, it can be tentatively concluded that decortication tends to facilitate hypothalamic activity and, from the present results, it follows that spreading depression or Nembutal applied topically inhibit such activity. Therefore, it can be deduced that the effect of decortication is not directly comparable with the effect of spreading depression. Since descending influences from the cortex appear to be mainly inhibitory, decortication brings chiefly facilitatory effects, while cortical anesthesia or spreading depression chiefly block a facilitatory mechanism. Cortical stimulation in certain places partially activates the inhibitory mechanisms. A similar effect was found by Feldman (1965), who observed that stimulation of the caudate nucleus produced an inhibitory influence on the hypothalamus.

SUMMARY

The present paper deals with the effect of cortical stimulation on exteroceptive evoked potentials in the dorsal hypothalamic area. The functional state of the cortex is significant for the activity of the hypothalamus. Cortical blocking by depressing agents induces a drastic modification of exteroceptive hypothalamic activity. Electrical stimulation of the cerebral cortex induces evoked activity and/or inhibition of the exteroceptive potentials in the hypothalamus, depending upon the cortical locus stimulated.

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THE EFFECT OF UNCONDITIONED AND CONDITIONED
STIMULI ON PERIODIC MOTOR ACTIVITY
OF THE STOMACH AND DUODENUM IN DOGS

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It has been shown for the first time in Pavlov's laboratory that the alimentary stimulation of the oral cavity during eating changed the movements of the stomach in dogs. Lintvarev (1901) observed such a phenomenon during both actual and sham feeding. Shirokikh (1901) noticed that the movements of an empty stomach were stopped for some time when the dog was fed with broth or milk. Cheshkov (1902) showed that the inhibition of the stomach movements, that occurs during sham feeding or actual food intake, is mediated by vagus nerves. An accelerated passage of liquids from the stomach to the intestines during sham feeding with milk and meat was observed by Best and Cohnheim (1910) and by Best (1911) in oesophagotomized dogs with gastric fistulae. Carlson (1912, 1913, 1916) showed that the mastication of tasteless substances (paraffin, rubber, etc.) by man with a constricted oesophagus and with a gastric fistula inhibits stomach movements to a smaller extent than the alimentary stimulation of the gustatory receptors. On the basis of experiments, performed on dogs, Carlson concluded that it was difficult to distinguish between the effects of mastication, swallowing or other acts on the movements of the stomach. It was shown by Alvarez (1928) that an inhibition of hunger contractions of the stomach in men occurred during eating of both palatable and tasteless food. When experimenting with an oesophagotomized dog with fistulae of the fundal and pyloric parts of the stomach and duodenum, Galperin (1929) showed that a continuous contraction of the prepyloric sphincter occurred during the entire period

of sham feeding with bones and pure sand. A brief contraction of the sphincter was observed during sham feeding with meat and pulverized dry bread and no contraction took place when the dog was sham fed with milk. Thus, the fundal part of the stomach was separated from the pyloric part during the mechanical stimulation of the receptors of the oral cavity.

The purpose of our present studies was as follows: (i) to study the effects of the stimulation of the oral cavity receptors on the contractions of the smooth muscles of the stomach and duodenum in the course of alimentary and acid unconditioned reflexes, and (ii) to investigate the influence exerted by alimentary conditioned stimuli (reinforced with either liquid or solid food) and by acid conditioned stimuli on the motor activity of the digestive tract.

MATERIAL AND METHODS

Chronic experiments were performed on 11 male dogs with the following operations:

No. of dog	Type of operation
1	Fistulae of the parotid gland and of the fundal and pyloric parts of the stomach.
2	Fistulae of the parotid gland and of the fundal part of the stomach.
3	Fistulae of the parotid gland and of the fundal part of the stomach and duodenum.
4	A fistula of the fundal part of the stomach. Afterwards — oesophagotomy.
5	Fistulae of the fundal part of the stomach and duodenum. Afterwards — oesophagotomy.
6	Fistulae of the fundal part of the stomach and of the duodenum.
7	A fistula of the fundal part of the stomach.
8	A fistula of the fundal part of the stomach and oesophagotomy.
9	A fistula of the fundal part of the stomach and an oesophagotomy.
10	A fistula of the fundal part of the stomach.
11	Fistulae of the parotid gland and of the fundal part of the stomach.

Recording of the masticatory movements of the lower jaw was effected by means of a specially constructed mask or muzzle with two elastics sewn into the thong encircling the animal's jaws. This allowed the dog to open his mouth when chewing. A rubber balloon, connected to a Marey's capsule, was attached below the mandible and enabled the kymographic recording of the movements of the jaw when the animal was masticating and swallowing. The movements of the stomach and intestines were recorded by an air-water transmission and by means of small rubber balloons which were introduced through fistular tubes and connected to Marey's capsules. Prior to connecting them with Marey's tubes, the balloons were filled with water at a temperature of 37—38°C. The balloons introduced into the fundal part of the stomach contained 80—100 ml, those introduced to the pyloric part — 25—35 ml, and those introduced to the duodenum — 8—15 ml of water. The salivation was recorded by means of an electrical recording device.

The experiments were performed within 18—22 hr after feeding. Ten to fifteen minutes before the experiment, both the stomach and duodenum were washed with water at a temperature of 25—30°C.

The results of some experiments on dogs fed with bones or soup were checked roentgenoscopically on oesophagotomized animals after introducing a contrast medium into a rubber balloon placed in the stomach.

According to the type of the periodic activity of their stomachs, the animals were divided into two groups. In the first group (dogs no. 1, 3—7, 10) slow, small contractions of the stomach, alternating with strong, rapid movements accompanied by an increased tonus of musculature were observed. In the second group (dogs no. 2, 8, 9, 11) small, contractions only rarely were replaced by strong, rapid movements and with a raised muscular tonus.

RESULTS

Unconditioned reflexes

The effect of fluid aversive substances and water introduced in the oral cavity. Dogs no. 1, 2 and 3 were used for 50 experiments during which 250 trials were given, consisting in an introduction to the oral cavity, by means of a special device, of 20—30 ml of 0.25% solution of HCl, 0.25% solution of NaOH or 10% solution of NaCl. In dog no. 1, within 10—20 sec after the introduction of aversive substances, in most cases, an increase of the hunger contractions persisting 1—2 min was produced in both the fundal and pyloric parts of the stomach. In other, rather rare cases, a decrease in the contractions was recorded. Identical results were obtained in dog no. 3 in which, in addition, a conspicuous increase was observed in the tonic contractions of the duodenum. On the contrary, in dog no. 2, in most cases, a brief inhibition of the movements of the fundal part of the stomach occurred within 5—10 sec (Fig. 1).

In 14 experiments, performed on dogs no. 2 and 3, prior to the application of aversive stimuli, water at room temperature was introduced into the oral cavity in 54 cases. As a result of these experiments, in both dogs considerably smaller changes occurred in the contractions of the stomach and duodenum and, in addition, they were quite different in character. In some cases, an increase in contractions and, in some others, an inhibition of the activity of the stomach and duodenum were observed.

The effect of solid aversive substances (sand) introduced to the oral cavity. Three dogs (No. 1, 2 and 3) were used for 18 experiments during which 59 trials were performed, consisting in pouring, by means of a test glass, of 8—15 ml of washed sand into the mouth. In all the dogs, within 15—30 sec after the onset of stimulation of the oral cavity, there occurred an increase in the contraction of the fundal and pyloric parts of the stomach and duodenum which persisted for 2—3 min on the average

(Fig. 2). Only in a few cases an inhibition or a two-phase reaction of the stomach (increase in activity, followed by inhibition) was observed.

The effect of sham feeding of oesophagotomized dogs with differently sized pieces of meat. The oesophagotomized dogs no. 4, 8 and 9 were used for 219 experiments during which they were sham fed with differently sized pieces of meat. These experiments showed that chewing of meat increased the contractions of the stomach and raised the tonus of its

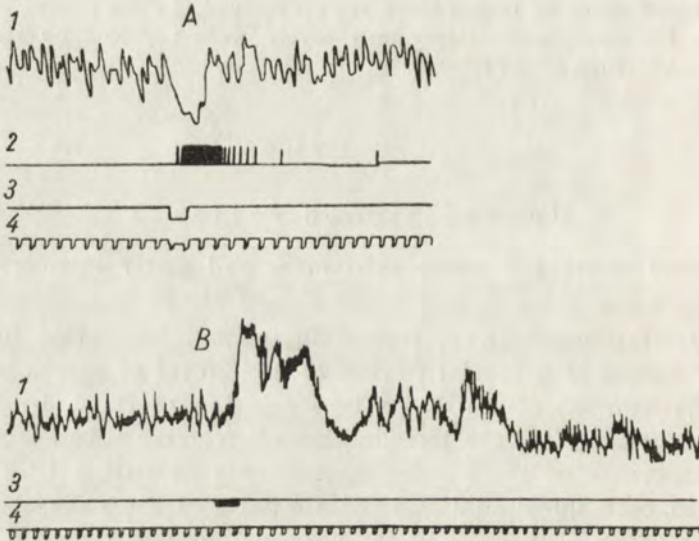


Fig. 1. Effects of introduction of acid into the oral cavity on the contractions of: A, fundal part of stomach in the dog no. 2; B, duodenum of dog no. 3. 1, contractions of stomach or duodenum; 2, salivation; 3, introduction of acid; 4, time (10 sec)

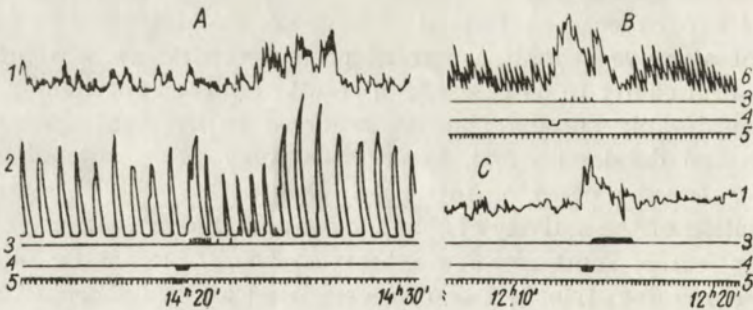


Fig. 2. Effects of stimulation of the oral cavity with sand upon the contractions of: A, fundal part of stomach in dog no. 3; B, pyloric part of stomach in dog no. 1; C, fundal part of stomach in dog no. 2. 1, movements of the fundal part of stomach; 2, respiration; 3, salivation; 4, introduction of sand; 5, time (20 sec); 6, movements of the pyloric part of stomach

muscles, while swallowing of the morsels elicited an inhibition of the contractions and a drop in the muscular tonus (Fig. 3 and 4).

The effect of normal and sham feeding with solid and liquid food. In seven dogs (no. 4-10) during 516 sessions normal or sham feeding with bones or soup (broth) was carried out for 1-2 min. Mastication

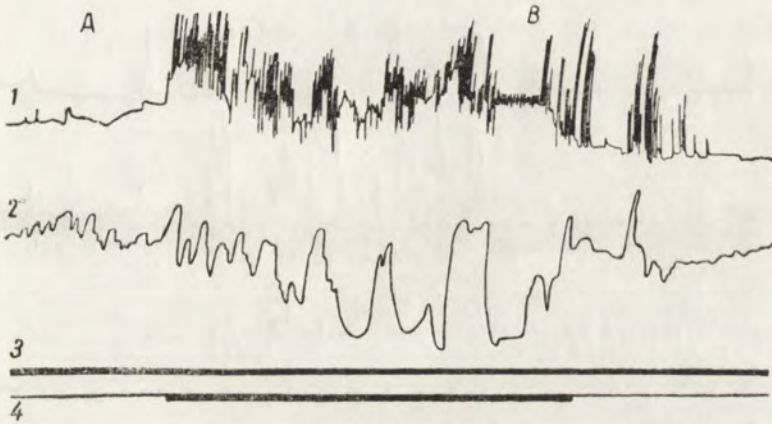


Fig. 3. Effects of mastication and swallowing during sham feeding of dog no. 4 with 100 g of meat. A, mastication; B, swallowing. 1, movements of the mandible; 2, contractions of the fundal part of stomach; 3, time (5 sec); 4, sham feeding

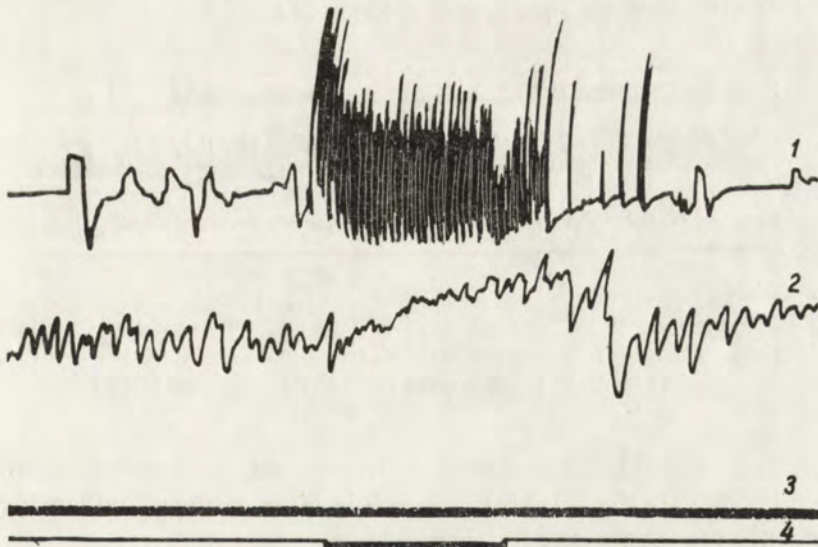


Fig. 4. Effects of a continuous strong mastication during sham feeding of dog no. 4 with 100 g of meat. 1, movements of the mandible; 2, contractions of the fundal part of stomach; 3, time (5 sec); 4, sham feeding

during sham feeding with bones evoked stomach contractions and an increase in the muscle tonus (Fig. 5), as well as a decrease in the intensity of duodenum contractions which ceased periodically. After eating up of the bones an increase was observed in the activity of the duodenum. Swallowing of the fluid food (soup) produced an inhibition and even a complete abolition of the stomach activity (Fig. 6). The movements

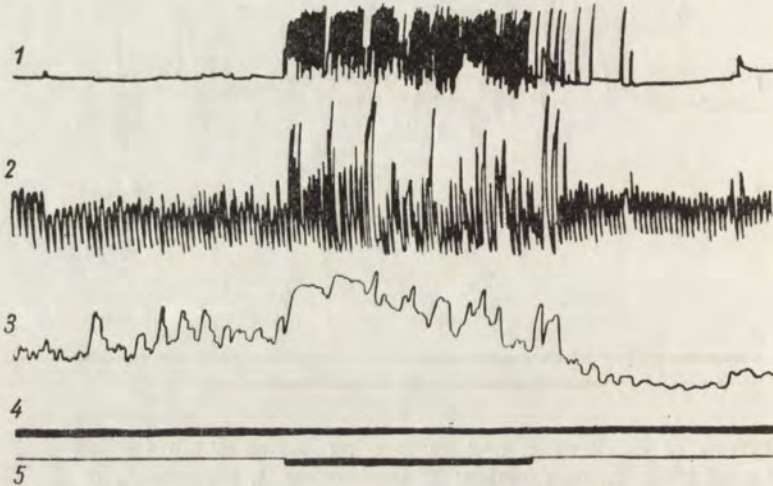


Fig. 5. Effects of mastication during sham feeding of the dog 9 with bones. 1, movements of the mandible; 2, respiration; 3, contractions of the fundal part of stomach; 4, time (5 sec); 5, eating of bones

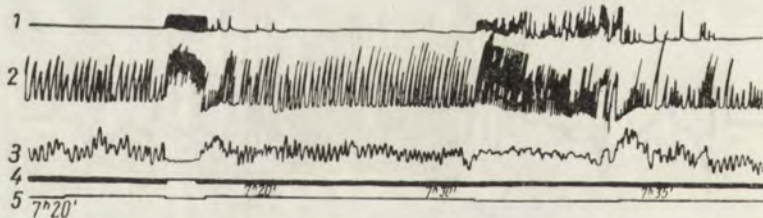


Fig. 6. Sham feeding of the dog no. 4 with soup and bones. 1, movements of the mandible; 2, respiration; 3, contractions of the fundal part of stomach; 4, time (5 sec); 5, sham feeding with soup (left) and bone (right)

of the duodenum during eating of the fluid food were either completely stopped or sharply decreased. Immediately after eating a sudden increase in this activity was observed.

Mechanical stimulation of the pharynx also produced an inhibitory effect on stomach contractions, whereas no effect at all was elicited by such a stimulation on the lower part of the oesophagus (Fig. 7 and 8).

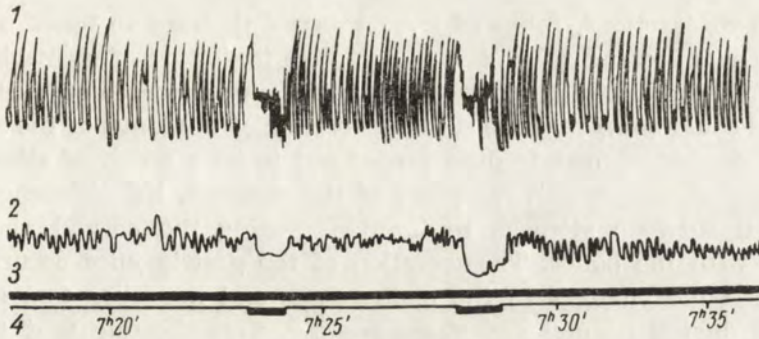


Fig. 7. Effects of swallowing during sham feeding with soup and mechanical stimulation of the pharynx in the dog no. 4. 1, respiration; 2, contractions of the fundal part of stomach; 3, time (5 sec); 4, left sham feeding with soup; right, stimulation of pharynx

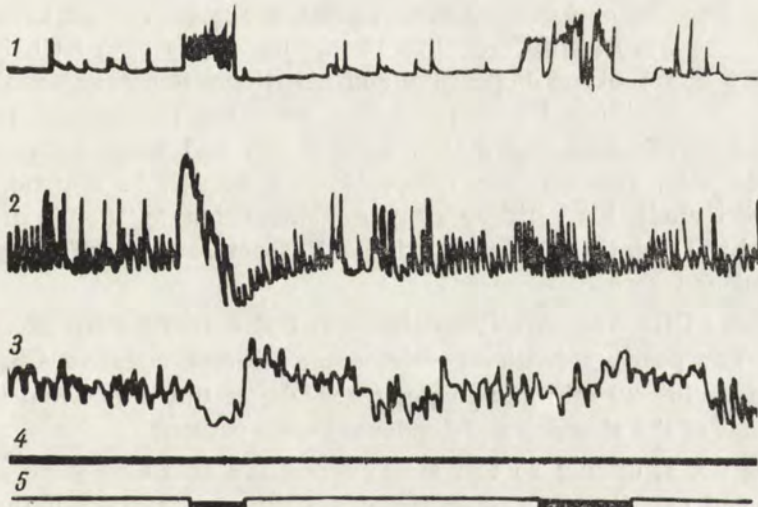


Fig. 8. Effects of the mechanical stimulation of the pharynx and of lower part of oesophagus in the dog no. 4. 1, movements of the mandible; 2, respiration; 3, contractions of the fundal part of stomach; 4, time (5 sec); 5, left, stimulation of pharynx; right, stimulation of oesophagus

Prior to the oesophagotomy, dogs no. 4 and 5 were normally fed with bones and soup. Sham feeding was performed on the same dogs after oesophagotomy, as well as on dogs no. 8 and 9. Dogs no. 6, 7 and 10 were fed normally. This allowed us to compare the results of the normal (5 dogs) and sham (4 dogs) feeding with bones and soup. We showed that during normal feeding with soup, there occurred a sudden inhibition of

stomach contractions, followed by a raise of the muscle tonus, whereas during sham feeding with soup, a complete inhibition of stomach movements combined with an attenuation of the tonus appeared at once. Moreover, we could show that the subsequent raise of the tonus of the stomach muscles during normal feeding turned out to be a result of stimulating with soup of the stretch receptors of the stomach. No difference could be found between stomach contractions during the normal and sham feeding with the bones. The secretion of the gastric juice occurs much later than the changes in the contractions and muscular tonus of the stomach during normal and sham feeding, thus showing that the two processes are independent of each other.

Conditioned reflexes

A stereotype of CRs was established in dog no. 1. It consisted of one positive alimentary CR reinforced with a mixture of powdered dried meat and bread-crumbs, and several positive and one negative acid CRs. Positive acid CRs were reinforced with 15—25 ml of the 25% HCl. In dogs no. 2 and 3 a stereotype of positive and negative alimentary conditioned reflexes was established and reinforced with the meat-bread powder. Intervals between alimentary CRs were 6 min and those between acid CRs 8—10 min. The CS—US intervals were 30 sec. In dog no. 2 the positive CS elicited a salivary response amounting to 10—11 drops of saliva and the negative CS to 2—3 drops. Respective figures for dog no. 3 were 7—8 and zero.

After the CRs were firmly established, test sessions were given once a week. The positive (without reinforcement) and negative CSs were presented at 10—20 min and longer intervals, at the time when hunger contractions of the stomach and duodenum were present.

In dog no. 1, during 25 test sessions positive acid CSs were applied 56 times and negative CSs — 36 times. On the presentation of the positive CS, the movements of the fundal and pyloric parts increased and muscular tonus was raised in 52 cases. No effect was observed in 4 cases. On the presentation of the negative CS, an increase was recorded in the stomach activity in 30 cases, a decrease — in one case and no effect — in five cases.

In dog no. 3, 88 positive alimentary CSs and 81 negative ones (differentiation and extinction) were given. Positive alimentary CSs as a rule stopped or decreased the movements of the stomach (decrease in 41 cases, increase in 2 cases and no effect at all in 3 cases) and increased the activity of the duodenum (increase in 30 cases, decrease in 3 cases, no effect in 9 cases) (Fig. 9).

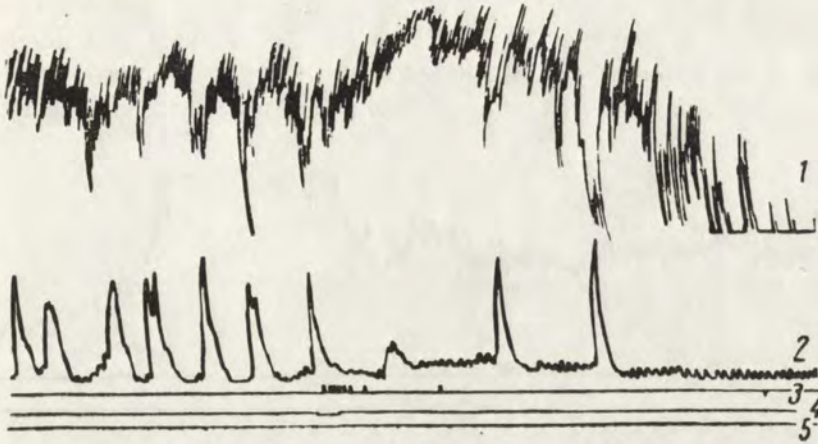


Fig. 9. Effect of a positive alimentary CS on the contractions of duodenum and fundal part of stomach in the dog no. 3. 1, duodenum; 2, fundal part of stomach; 3, salivation; 4, sound of bell (positive CS); 5, time (10 sec)

Negative alimentary CSs in most cases increased the contractions of the stomach and the tonus of the duodenum (stomach: intensification in 32, decrease in 2 and no effect in 8 cases; duodenum: intensification in 29, decrease in one and no effect in 9 cases) (Fig. 10).

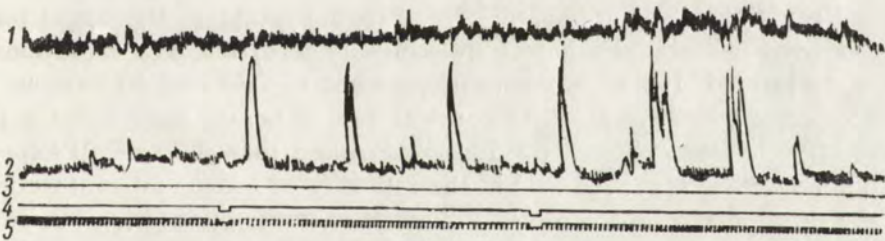


Fig. 10. Effect of a negative alimentary CS (differentiation) on the contractions of duodenum and fundal part of stomach in the dog no. 3. 1—3, see Fig. 9; 4, sound of bell (negative CS); 5, time (10 sec)

The same effects of positive and negative alimentary CSs on the activity of the stomach were obtained in the experiments performed on dogs no. 1 and 2 (Fig. 11).

In dogs no. 4, 5, 6 and 7, conditioned reflexes were established by reinforcing the CSs with either soup or bones. A CS was presented for 30 sec and then followed by a 1 min food intake. CRs to the sound of a bell, reinforced by the presentation of the bones, were established in

the oesophagotomized dog no. 4 with a fistula of the fundal part of the stomach and in dog no. 6 with fistula of the stomach and duodenum. A CR to the sound of a bell, reinforced by the presentation of the soup, was established in the oesophagotomized dog no. 5 with fistulae of the

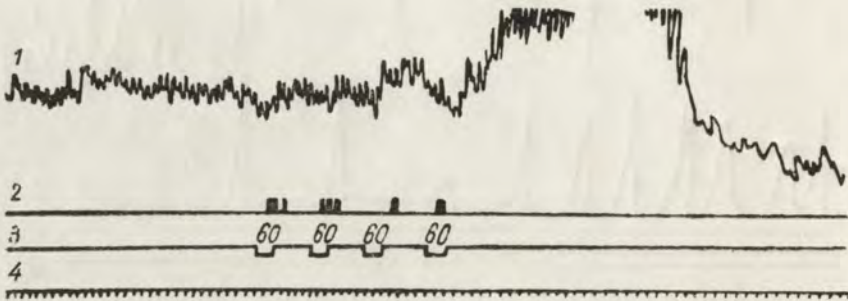


Fig. 11. Effect of extinction on the contractions of pyloric part of stomach in dog no. 1. 1, pyloric part of stomach; 2, salivation; 3, sound of a metronome (60 beats per minute), a negative CS; 4, time (10 sec)

fundal part of the stomach and duodenum and in dog no. 7 with a fistula of the fundal part of the stomach. After the CRs were well established, the test trials were given in which the CSs were presented without reinforcement. Afterwards, in the first two dogs, CRs were established to the sound of a bugle reinforced by the presentation of the soup and in the remaining two animals — those to the sound of the bugle reinforced with the presentation of the bones. Thereafter, 172 experiments were performed, 142 with the reinforcement of CSs and 30 without it. In all cases, the CS signalling presentation of bones, gave exactly the same effect as that elicited by the US: in more than 30% of all experiments a decrease was produced in the intensity of individual contractions of the stomach accompanied by an average or (more often) high muscular tonus (Fig. 12). It decreased the intensity of single contractions of the duodenum while producing their periodical cessations.

To study the CSs signalling the presentation of fluid food (soup) 205 experiments were made of which 172 were performed with the reinforcement of CSs and 33 without such reinforcement.

The CS signalling soup fully reflected the unconditioned activity of the stomach muscles. Namely, in oesophagotomized dogs it evoked the cessation of the stomach movements, followed by the decrease in the tonus of the muscles (Fig. 13) and, in non-oesophagotomized animals, it produced a characteristic cessation of the stomach movements, followed by a staircase-like raise of the tonus of the stomach muscles. At the same time, the CSs, reinforced by presentation of soup, elicited complete or

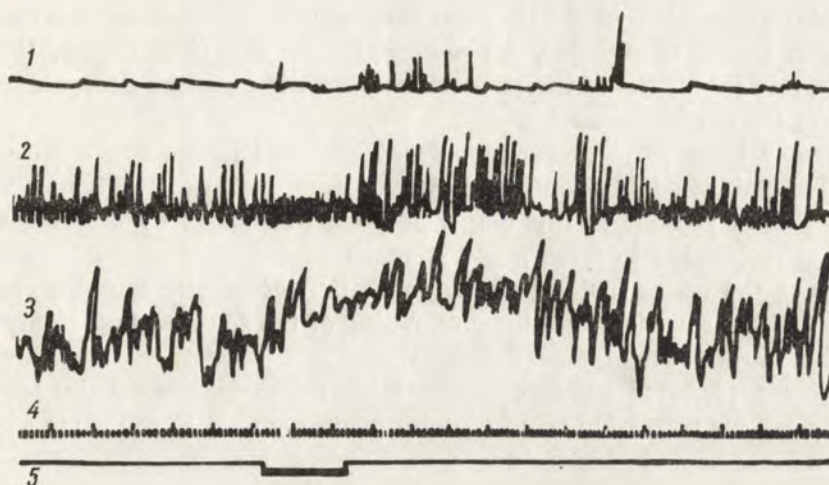


Fig. 12. Effect of a positive alimentary CS normally reinforced by feeding bones in the dog no. 7. 1, movements of the mandible; 2, respiration; 3, movements of the fundal part of stomach; 4, time (3 sec); 5, sound of bugle (positive CS)

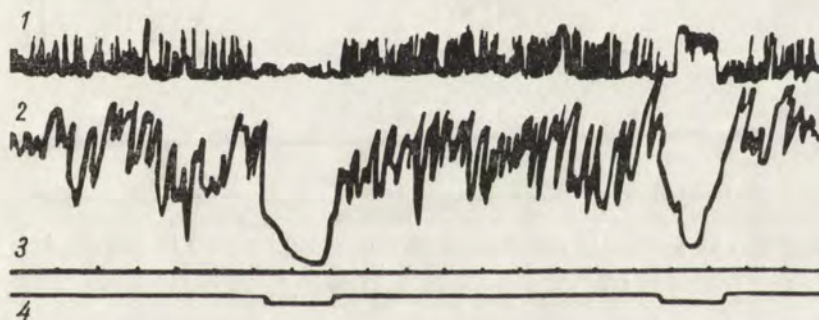


Fig. 13. Effect of a positive alimentary CS (normally reinforced by feeding soup) and of the act of eating of soup. Dog. no. 7. 1, respiration; 2, movements of the fundal part of stomach; 3 — time (20 sec); 4, left, sound of bell, signalling soup; right, eating of soup

periodical cessation of the movements of duodenum, followed, directly after eating, by a sudden increase in its activity.

In non-oesophagotomized dogs, the CSs signalling soup evoked a usual complex reflex, that is, a typical inhibition of the stomach muscles, observed during the stimulation of the receptors of the oral cavity during eating of the soup, as well as another reflex, that is, an increase of the muscle tonus of the stomach observed at the moment when the soup reached the stomach. In the oesophagotomized animals, in contradistinction to the non-oesophagotomized ones, on the application — without

the reinforcement — of the CS signalling soup in the predominant number of cases (more than 75%), we observed only the first reflex, that is, a complete inhibition of the stomach movements with the decrease in the tonus of the stomach muscles.

A very interesting phenomenon was observed in the dog with a previously established CR reinforced by the presentation of the bones. When we began to present to this dog a new CS reinforced by offering soup, the dog responded to it with the stomach contractions characteristic for eating of the bones instead of the relaxation of gastric muscles characteristic of the soup intake. Likewise, eating of the soup evoked an atypical effect of eating of the bones (Fig. 14).

After a repeated reinforcement of both CSs (of eating the soup or the bones), we presented them without reinforcement in the same experi-

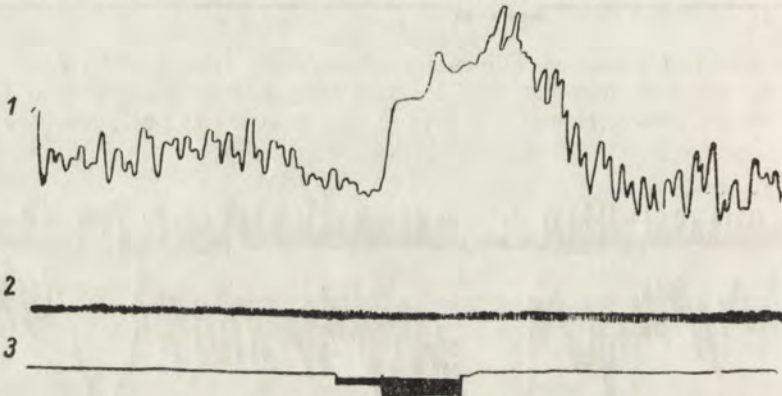


Fig. 14. Effect of a recently established CS reinforced by soup in dog no. 4. 1, movements of the fundal part of stomach; 2, time (3 sec); 3, sound of bugle a CS, reinforced with the soup intake

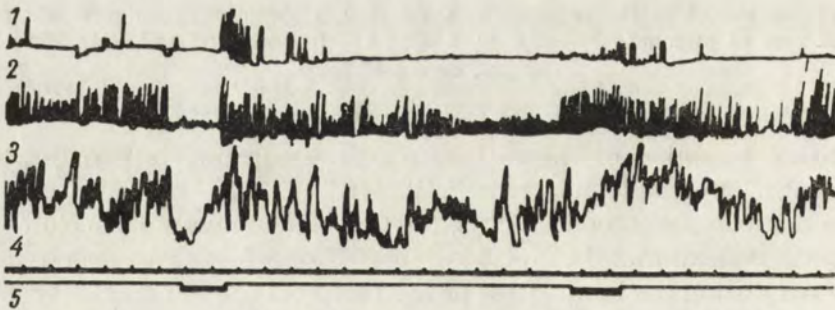


Fig. 15. Effect of the positive alimentary CSs signalling food of different consistency. Dog. no. 7. 1, movements of the mandible; 2, respiration; 3, movements of the fundal part of stomach; 4, time (20 sec); 5, left, sound of bell, signalling soup; right, sound of bugle signalling bones

mental session at 15—20 min long intervals. In this series we performed a total of 302 experiments. Of this number, in 268 cases the CSs were reinforced with the soup or bones and, in 34 cases, they were presented without reinforcement.

The bell and the bugle, presented in a session without reinforcement, elicited different changes in the periodic hunger contractions of the stomach and duodenum, depending on the signalling character of each of these stimuli (Fig. 15).

CONCLUSIONS

We succeeded in showing that the stimulation of the oral cavity of the dogs with aversive and alimentary substances evoked regular changes in the periodic hunger contractions of the stomach and duodenum.

Fluid aversive substances, introduced into the oral cavity of two dogs, in most cases intensified the contractions of the fundal and pyloric parts of the stomach and, in a few cases, inhibited this activity. In one dog an opposite phenomenon was observed, that is, in most cases these substances inhibited the contractions of the fundal part of the stomach and, only in a few cases, intensified them. This was, however, true only in the stomach, whereas the contractions of the duodenum were mostly intensified by these substances.

Two kinds of effects, that is, the intensification and inhibition were obtained by the application of the water at room temperature. Mechanical stimulation of the oral cavity mostly intensified the contractions of the fundal and pyloric parts of the stomach and duodenum.

When a dog was eating meat, the mastication elicited an increase in the activity of the fundal part of his stomach and swallowing of this food produced an inhibition.

The mastication of bones intensified the periodic contractions of the stomach and raised the tonus of its muscles at the same time, decreasing the amplitude of the contractions of the duodenum, now and again, even evoking the cessation of its activity and, after the food intake, intensifying it. Swallowing of a fluid food (soup) inhibited and even fully stopped the periodic activity of the stomach and, at the same time, inhibited or stopped the movements of the duodenum, suddenly intensifying them, however, after the food intake. It was shown that, during normal eating of the soup, after a rapid inhibition of stomach contractions, evoked by the stimulation of the receptors of the oral cavity, there occurred a successive increase in the tonus of the stomach, elicited by the stimulation of its receptors. Such a successive increase in the tonus of stomach muscles was not observed in the oesophagotomized animals. During both

the normal and sham feeding with bones no differences in stomach contractions were manifested.

Positive CSs, signalling aversive substances, intensified the contractions of the fundal and pyloric parts of the stomach and increased its tonus. Negative CSs with regard to aversive substances also increased the motor activity of the stomach.

Positive alimentary CSs, reinforced with powdered dried meat and bread, elicited, as a rule, a cessation or a decrease of the movements of the stomach and an increase in those of the duodenum. Negative alimentary CS (differentiation, extinction) in most cases intensified the contractions of the stomach and duodenum.

When applied without the reinforcement and against the background of the hunger contractions of the stomach and intestines, positive CSs, previously reinforced many times with bones or soup, evoked characteristic changes in the activity of the stomach and duodenum corresponding to the character of the unconditioned stimulus.

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FUNCTIONS OF THE CAUDATE NUCLEUS¹

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According to Wilson's early review (Wilson 1913/14), for three hundred years we have known that the caudate nucleus (NC) exists and for about half that time it has been examined experimentally. Four recent reviews summarize the data accumulated till now both from the clinical and experimental viewpoints. Two of them (Jung and Hassler 1960, Denny-Brown 1962) claim that the NC function is related to motor mechanisms, and the other two arrive at different conclusions. Laursen (1963) believes that the NC may be involved in learning and emotional processes, whereas Cherkes (1963) says that the role of the NC cannot be formulated at present.

All four reviews as well as almost all of the literature covered have one assumption in common: that the NC is functionally equipotential. Even the authors who would agree that NC has more than one function, assume generally that the possible different mechanisms for such functions are evenly distributed throughout the NC. Tacitly, the histological uniformity of the NC was taken to imply its functional homogeneity. In the present paper another point of view is presented based on more recent results.

It is hypothesized that the neostriatum performs the same behaviorally defined functions as the cortex but on a different „level”, the „levels”

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being respectively dependent on the position of the species in the evolutionary scale. The idea is not a new one, Swedenborg in 1740 said (Swedenborg 1882) that corpora striata are vicarious cerebra, but now it seems possible to substantiate it.

The hypothesis can be divided in the following two postulates: (i) The neostriatum is a level in Jacksonian terms. It is more primitively organized than the cortex and with the development of cortex becomes dominated by it to the degree to which „corticalization” has advanced in the species. (ii) The neostriatum has many functions located in its different parts, perhaps as many as the cortex and related to cortical functions, but not necessarily identical qualitatively or quantitatively with them. The adequate cue to tell different subareas of the neostriatum apart are the cortico-neostriatal connections. The hypothesis contains the assumption that there are no greater differences between the NC and putamen than there are between regions within them. This assumption is based only on deductions from phylogenetic, embryological and histo-morphological material. The NC and putamen are seen to differ only in so far as their cortical inputs differ.

The above postulates are supported by the data which will be first grouped and then discussed in turn. The first postulate is based on the facts that: (i) There exists a level of phylogenetic development in which the striatum is the „highest” formation of the brain. (ii) The complexity of behavior of a totally decorticated animal with the striatum preserved („striate animal” of Wang and Akert 1962) is somewhere in between that of the normal and „thalamic” animals. (iii) The NC is coupled to all sensory modalities and also is able to regulate motor and autonomic processes.

The data that support the second postulate are: (iv) Different parts of the NC behave differently, or could be shown to have different functions. (v) The respective cortical and NC regions were found to subservise the same function although not necessarily with the same proficiency. (vi) Cortical and the respective NC regions are anatomically connected.

SURVEY OF DATA

1. *There exists a level of phylogenetic development in which the striatum is the „highest” formation of the brain.* The existence of such a species, able to display a variable behavior which would require possession of various „capacities” and „functions”, supports the assumption that the neostriatal structure is sufficient and versatile enough to integrate that behavior and make it more complex than the behavior of a species having no neostriatum.

Comparative anatomy describes reptiles and birds as that level of phylogenetic development in which only very restricted and primitive cortex can be found. In other words, corpus striatum is their highest integrative structure. Admittedly, this argument is not very strong because it cannot be claimed that the striatum in birds or reptiles is identical with that of mammals.

2. *The complexity of behavior of a totally decorticated animal with the striatum preserved is somewhere between that of the normal and „thalamic” animals.* The topic discussed in this section is whether the striatum represents a „level” in the organization of the brain having a well developed cortex, i.e., could it function independently from the cortex.

It can be stated that the behavior of a striate animal depends on the position of the observed species in the phylogenetic scale. Wang and Akert (1962) reviewed earlier results and described the behavior of striate and thalamic cats concluding that the striate animals have much better organized behavior which in simple situations can almost be indistinguishable from that of normal animals³. On the other hand, Fulton (1951) said that „there is little to differentiate a decorticate primate from a thalamic or hypothalamic preparation”. In other words, comparison between the decorticated cats and monkeys suggests an advanced „corticalization” in monkeys, or, on the other hand, a relatively smaller dependence of the striatum on cortical functioning in cats. It is important to point out that decortication does not result in a cell loss in the NC (Burandt et al. 1961, Wang and Akert 1967). The only report describing a contrary finding is that of Harman et al. (1954).

Additional evidence that the NC has functions to some extent independent from cortical functioning comes from the following studies: Cherkes (1963) described movements from the NC stimulation 30 days after the removal of the motor areas in the dog. However this is perhaps too short a period to exclude the possibility of producing the movements by actually stimulating the pyramidal fibers which degenerate up to twelve months after the cortical lesion; Russell and De Meyer (1961). Sadowski and Traczyk (1963) reported that a unilateral decortication in the rabbit did not influence the rate of acquisition of the conditioned response in which the NC stimulation of each side separately was used

³ The term „thalamic” is somewhat confusing. It may indicate the formation, above which everything has been surgically removed, and on the other hand, it may imply the highest remaining level of the function which has been preserved. The second meaning is incorrect in this case because of the cell loss in the thalamus after the removal of the telencephalon. In that, second, sense the „thalamic level” does not exist.

as the conditioned stimulus. Weiss and Fifková (1963) observed that the circling behavior obtained by a unilateral NC lesion in the rat is not changed by cortical spreading depression on either hemisphere.

These results together with the observations of the decorticated animals suggest that the striatum has its proper functions which may be to some extent independent of cortical integrity and which may represent an important level in the organization of behavior.

3. *The NC is coupled to all sensory systems, and also is able to participate in regulation of the motor and autonomic processes.* If neostriatum represents a „level” in the organization of the brain, it should have its own sensory, motor and autonomic mechanisms similar to those the cerebral cortex has. These mechanisms, although related to the corresponding cortical mechanisms, should have some independence.

It is established anatomically that the nonspecific thalamic nuclei: centralis medialis, paracentralis and centralis lateralis project to the NC, while centrum medianum projects to the putamen (Drogleever-Fortuyn and Stefens 1951, Cowan and Powell 1955, Powell and Cowan 1956, Johnson 1961). In agreement with this, the electrophysiological evidence shows a convergence of various sensory modalities on the NC neurons (Albé-Fessard et al. 1960b). This can be interpreted as showing that sensory input reaches the NC, although in a diffuse manner. Moreover, it has been shown that the appearance of the NC evoked potentials is independent of the integrity of the cortex (Albé-Fessard et al. 1960a).

It is a classical notion that the NC is involved in regulation of posture and movements and although it is perhaps too narrow to consider the NC as a formation exclusively regulating motor functions, some motor role cannot be denied. Both sensory and motor coupling of the NC are not identical with those of the cortex, e.g. „pyramidal” in the cortex and „extrapyramidal” in the basal ganglia. This is, however, in agreement with the idea of a different „level” of the NC functioning contained in the present hypothesis.

Almost all kinds of autonomic effects were obtained with the NC stimulation, but on the basis of Laursen's (1963) studies they could be attributed to the current spreading to the septum. Rosvold and Delgado (1956), however, after lesions of the NC, reported gastrointestinal disturbances: retching, vomiting and anorexia lasting about a week. Wang and Akert (1962) reported differences in galvanic skin response (GSR) measurement in striatal and thalamic cats. In the striate cats the GSR was observed, but not in the thalamic cats. It can be summarized that the NC receives a diffuse sensory input without cortical mediation and that it participates in regulation of the skeletal muscle tone and movements as well as of autonomic functions.

4. *Different parts of the NC behave differently, or could be shown to have different functions.* If the neostriatum is „the vicarious cerebrum” it has to subserve many functions as the cortex does. Its functional heterogeneity is the essential item of the present hypothesis. The question of the heterogeneity of the NC has not been at issue due, perhaps, to the histological homogeneity, in the sense that the cytoarchitectonics of the NC did not bring about divisions in areas as it did in the cortex, to the absence of somatotopic organization (Mettler et al. 1939, Albé-Fessard et al. 1960ab), and perhaps most of all to the absence of a key to analyse the NC regionally. Very few authors explicitly claimed the heterogeneity of the NC (Grastyan et al. 1953, Cherkes 1963, Divac et al. 1967), there are many data, however, which point to it.

The anatomical heterogeneity of the NC is suggested not only by cortico-NC connections (see below) but also by preliminary studies of the myeloarchitectonics of the NC in the dog (Nowak, in preparation).

Biochemically, oxydative enzymes are unevenly distributed in the neuropil of the NC. A very similar picture is seen in the cortex (Friede 1966). It is not known whether the corresponding cortical and NC regions have a parallel activities of the oxydative enzymes.

Many data obtained by stimulation of the NC indicating a heterogeneity of function may be considered doubtful because of the effects of anesthesia and spread of current (Laursen 1963); they will be, however, listed here for the sake of completeness. A series of studies in which various aspects of inhibition were observed revealed that most often the basolateral part of the NC was effective in eliciting inhibitory effects. Thus, Cherkes (1963) found that the spontaneous movements in cats can be inhibited by stimulation of the ventrolateral part of the NC. Hankinson et al. (1955) included the external part of the NC in their descending inhibitory system. Grastyan et al. (1953) found that movements induced by cortical stimulation can be facilitated from the dorsomedial, and inhibited from the basolateral parts of the NC in the cat. D'Anna and Krauthamer (1964) obtained inhibition of the „associative” cortical evoked potentials with stimulation of the dorsolateral NC. These authors suggest that the described NC area is a part of a descending inhibitory system starting in inhibitory cortical regions. Demetrescu and Demetrescu (1962) also stated that not all points in the NC were effective in eliciting inhibition of evoked potentials. Finally, Rubinstein and Delgado (1963) reported that with stimulation of different NC areas various inhibitory effects could be obtained in chronically implanted monkeys.

Heterogeneity was also found in respect to autonomic phenomena, muscle spindle discharges, skeletal muscle movements, and the delayed response performance. Mihailović (personal communication) observed

dissimilar autonomic responses with stimulation of different NC regions. Granit and Kaada (1952) obtained a shortlasting facilitation of gamma motor activity with stimulation of the rostromedial part of the NC, the same area which, according to Peacock and Hodes (1951) facilitates cortically-evoked movements. Forman and Ward (1957) described movements of anterior and posterior extremities evoked with stimulation of the anterior and posterior regions of the NC respectively. Cianci (1965) stimulated various points of the NC in monkeys during delayed response performance and observed that the stimulation of the dorsal points but not of the ventral points impaired performance.

More convincing in showing the NC heterogeneity are the data in which other formations were stimulated and effects recorded in different NC parts. Thus, Adey and Dunlop (1960) found that only the ventral cells of the NC were responsive to the combined stimulation of the amygdala and sciatic nerve. Furthermore, according to Butkhusi (1965), the shape, latency, and amplitude of evoked potentials in the NC during cortical stimulation were dependent on the electrode localization both in the cortex and in the NC.

Olds and Olds (1963) demonstrated that not all points in the NC were equivalent in respect of self-stimulation reinforcing properties.

Data obtained with local chemical stimulation also indicate heterogeneity. It was reported by McLennan and York (1966) that the cells in the dorsomedial part of the NC were excitable with microelectrophoretically applied acetylcholine or with stimulation of the ventral anterior thalamic nucleus, while the ventro-laterally placed cells were inhibited with the same agents. Ernst and Smelik (1966) reported that application of dopamine into a restricted area of the rat NC elicits compulsory gnawing. Divac et al. (1967) demonstrated recently that selective lesions of the NC in the monkey result in dissimilar effects. The latter results agree with the Cianci's stimulation data. Finally, Divac (1968) partially confirmed the differential effects of partial NC lesions in the cat.

All these data support the notion of the heterogeneity of the NC but presently are far from fitting together into an understandable whole.

5. *The respective cortical and NC regions were found to subservise the same function although not necessarily with the same proficiency.* The present hypothesis states that a NC area is defined by its cortical input. Such an area has a function which is similar to the function of the anatomically related cortical area. Two specifications are needed here: First, the anatomical relation is materialized in the direct connections between the related cortical and NC areas. Second, by the similarity of the function it is meant what the respective cortical and NC regions are doing rather than how they do it. We are able to define „what” only

operationally at present. In other words, the function is „motor” or „sensory” or „function of the delayed response behavior” etc. The question which arises here is: what is the relationship between the functions of the corresponding NC and cortical areas; are their functions identical, complementary, hierarchical or related in some other way?

Up to the recent time only differences, both morphological and functional, between the cortex and the neostriatum have been noted. Histologically, the two formations appear quite different from each other. Furthermore, there is a striking difference in the sensory and motor organization: the NC lacks both the primary somatotopical sensory projections, as reported by Albé-Fessard et al. (1960ab), and a more direct relationship with the bulbospinal motoneurons. The latter statement is based on the anatomical data: Voneida (1960) and Szabo (1962) showed that the NC projects to the pallidum and the substantia nigra. Studies of the pallidal efferents by Nauta and Mehler (1966), as well as of nigral efferents by Afifi and Kaelber (1965) in the cat and Carpenter and McMasters (1964) in the monkey did not reveal projections to the bulbospinal motoneurons.

From the functional point of view, in higher mammals the NC lesions do not cause paresis as compared to the effects of the motor cortical lesions. Parallely, the NC stimulation is not effective in producing discrete movements. The contrary results obtained by Forman and Ward (1957) are interpreted as due to the spread of current to the neighboring parts of the capsula interna. This may be understood as showing that the caudate counterpart of the motor cortex performs its motor function in a way dissimilar to the function of the motor cortex itself.

All these data point to the morphological and functional differences between NC and cortex. On the other hand, several papers appeared recently showing that the behavioral effects of restricted cortical lesions were replicated by the restricted NC lesions in different species. It is known that bilateral prefrontal cortical lesions result in the deficits of the delayed response (DR) and delayed alternation (DA) (see the volume edited by Warren and Akert 1964). Rosvold and Delgado (1956) were first to report the same deficit after the stimulation or lesion of the NC head in the monkey. Also in the monkey, Divac et al. (1967) demonstrated that the behavioral deficits obtained with selective cortical lesions can be replicated by the selective lesions of the corresponding parts of the NC. These authors found that the lesion in an anterodorsal NC region, which receives projections from the laterofrontal cortex, resulted in a DA deficit, whereas lesion in a ventrolateral NC region, receiving projections from the orbitofrontal cortex, gave rise to an object-reversal deficit. The only visual discrimination deficit, closely related to the damage of the

inferotemporal cortex (Mishkin 1954), was produced with a lesion of the NC tail which is known to receive projections from that cortical area (Whitlock and Nauta 1956). In a further study, Divac (1968) observed a DR deficit in cats after a lesion of the NC area which, according to Webster (1965), receives projections from both the proreal and orbital gyri.

Fox et al. (1964), also in the cat, found after a lesion of the NC area connected to the subcallosal cortex, a deficit similar but not identical to the deficit seen after the lesion of the subcallosal cortex itself. In the rat, Gross et al. (1965) obtained similar deficits after either frontal cortical or NC lesions in a version of an alternation task. Battig (1963) found an increased normal tendency to choose the alternate path in a modified T-maze both in the frontal cortical and in the NC lesioned rats. Interpretation of the results in rats is, however, difficult because the NC lesion inevitably produces an interruption of cortical fibers going through the neostriatum and therefore what is observed may be an effect of a double, cortical and NC lesion.

The question of whether in subserving a function the contributions of cortical and corresponding NC areas are equivalent is difficult to answer. It may very well be that in the same species, in different „cortico-NC systems”, variable degrees of contribution can be found. Only future work which will respect the NC subdivision can answer that question. At present it can only be said that functionally the cortical sensory-motor zone differs from the hypothesized „caudatal sensory-motor zone”. The results showing an unequal contribution in other cortico-NC systems should be reexamined, but let us mention them here. For instance, the NC lesion in the Fox et al. (1964) experiment did not exactly replicate the effects of the corresponding cortical lesion. There is also a suggestion that prefrontal cortex in the monkey is relatively more important for the DR than the prefrontal cortex in the cat (Divac 1968).

6. Cortical and the respective NC regions are anatomically connected.

The cortico-NC connections can be regarded to be the mediators of the joint action of the related areas of cortex and NC. If the whole cortex projects topically to the neostriatum, then all of the various functions of the cortex might be replicated in the respective parts of the NC.

An almost point to point correspondence between cortex and neostriatum has been described for the rat (Webster 1961), rabbit (Carman et al. 1963), and cat (Webster 1965). There is no complete study on the monkey, but papers on that topic show that not all cortical areas appear to project to the neostriatum. Thus, Nauta (1964) found that laterofrontal cortex projects to the anterodorsal part of the NC, and the orbitofrontal cortex

projects to the ventrolateral part of the NC. Whitlock and Nauta (1956) described projections from the inferotemporal cortex to the tail of the NC and the nearby part of the putamen. Areas 4 and 6 have also been found to project to the NC and putamen (Petras 1964) but Astruc (1964), could not find projections of the NC after the area 8 lesion.

The existence of the NC-to-cortex projections is still doubtful. Nauta-Gygax method employed by Voneida (1960) and Szabo (1962) did not reveal those projections. Krnjević and Silver (1965, 1966), however, by staining fibers with Koelle method which detects acetylcholinesterase, described fibers ascending from the NC to the cortex in cats. Shute and Lewis (1963) reported analogous findings for the rat.

It should be noted that the once fashionable idea of the suppressor cortical areas projecting to the NC is based on strychnine neuronography and should not be confounded with the anatomical findings. The neuro-nographical data do not exclude the possibility that other cortical areas project to the NC, perhaps to other regions of it.

DISCUSSION

In the present hypothesis, the first postulate attempts to establish the neostriatum as a separate level of integration having sensory, motor and autonomic functions not necessarily dependent on the existence of the cortex. If this „horizontal” separation in the two levels, cortical and neostriatal, is accepted, then automatically the idea of caudate nucleus being concerned only with motor functioning, or inhibition or for that matter any function that was proposed as the caudate function, becomes untenable. It becomes obvious that a new level must subserve many functions and the question remains only: are these functions represented diffusely or localized in different parts of the neostriatum. The apparent absence of a topical sensory and motor organization is still compatible with the very organized function as shown in Herrik's examinations of the nervous system of Tiger Salamander. Thus, without the material presented in order to support the second postulate, both diffuse and topical organizations are feasible.

The second postulate, however, takes the position that, in spite of an absence of cytoarchitectonic differences, the neostriatum is topically organized in the sense that probably the same mechanism, as defined by the neostriatal microstructure, subserves different functions. The scarce evidence that has been collected (Divac et al. 1967, Divac 1968) suggests that the cortex may be used as an indicator of the neostriatal division. In this „vertical” dividing, it is supposed that each function is subserved

by a pair of regions, cortical and neostriatal. The question remains open: does the cortex impose its division on the neostriatum, or the neostriatum has a topical organization of its own.

Various data suggest both similarities and differences between functions of the respective cortical and NC regions. The idea of an identity of functioning must be rejected on the basis of the existing dissimilarities.

Another possibility, that separate complementary functions necessary for the performance of the same task are localized in the two formations must also be abandoned because a decorticate cat possesses to a certain degree all the functions needed for behaving although on the more primitive level. Therefore it seems that the only possible way of understanding the accumulating evidence of the yoked functioning of the connected cortical and NC regions is to consider their functions as hierarchically organized.

It may be interesting in the present context to direct our attention to the interesting parallelism between the results of neodecortication in monkeys and cats (see survey of data, Section 2) with the results of only prefrontal ablation (see survey of data, Section 5), in both cases the cortical removal in the cat caused a smaller effect. Such parallelism adds weight to each individual comparison suggesting the importance of considering the phylogenetic factor in the analysis of results.

If the cortex is visualized as an agglomeration of fields subserving different functions at a high level of complexity, then the NC can be also considered to be a cluster of regions connected with the respective cortical fields subserving the same functions but with a lower level of proficiency. The relationship between the respective cortical and NC regions should be experimentally worked out for every pair of regions and in different species.

A word of warning is needed here: the possible inconsistencies in future experimental results could be explained by considering output connections of the NC going downwards, or by taking into account the passing fibers, or the fibers arriving from other formations which, as a myeloarchitectonical study shows (Nowak, in preparation) can also be selectively distributed. The same study also shows the presence of fibers going through the NC itself playing possibly a role of association fibers for different NC regions.

To conclude, we believe that subdividing larger structures in smaller units, a tendency which appeared with Fritch and Hitzig (1870) in the cerebral cortex, with Bolk (1902) in the cerebellar cortex, and now is to be found in hippocampus (Jarwie 1967) and NC (Divac et al. 1967) indicates progress in understanding brain mechanisms.

SUMMARY

The hypothesis that neostriatum has many functions as well as cortex, and that interconnected parts of cortex and neostriatum subserve the same behavioral functions probably at different levels has been advanced and discussed. The functional heterogeneity of the neostriatum is considered to be the most important aspect of the present hypothesis.

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STUDIES ON THE HYPOTHALAMUS OF THE DOG

II. INTERMEDIATE (TUBERAL) PART

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This paper is concerned with a myeloarchitectonic analysis of the nuclei of the intermediate (tuberal) part of the hypothalamus of the dog. The intermediate part consists of the region which is sometimes called the tuber cinereum (Morgan 1930, Clark Le Gros et al. 1938, Bleier 1961, Diepen 1962) and the dorsal nuclei of the hypothalamus, which have not always been included in it (dorsomedial nucleus, dorsal nucleus, dorsocaudal nucleus and posterior lateral nucleus).

Ten nuclei have been distinguished in the area under study; these are: (i) ventromedial nucleus, (ii) infundibular nucleus, (iii) posterior supraoptic nucleus, (iv) periventricular area, (v) ventrolateral nucleus, (vi) tuberomammillary nucleus, (vii) posterior lateral nucleus, (viii) dorsomedial nucleus, (ix) dorsal nucleus and (x) dorsocaudal nucleus.

As a distinct nucleus I regard an area marked by a uniform structure of fibres and uniform connections.

MATERIAL AND METHOD

The present paper is based on observations of eight continuous series of dog brain sections. Three series of sections, stained by Weigert-Wolters method (frontal, horizontal and sagittal) and transected every 50 μ , and five series, stained by the Klüver-Barrera, Nissl and Schultze method (two frontal, two horizontal and one sagittal) and transected every 20 μ were used for observations.

OBSERVATIONS

The boundary between the intermediate and anterior hypothalamus is marked out by a system of fibres of the supraoptic commissures. The caudal portion of the intermediate part reaches nearly as far as the mammillary bodies. Its boundary with the mammillary bodies is easy to define, especially in sagittal sections stained by Weigert-Wolters method, because the mammillary bodies are separated sharply from the adjoining hypothalamic structures by their capsule of myelinated fibres.

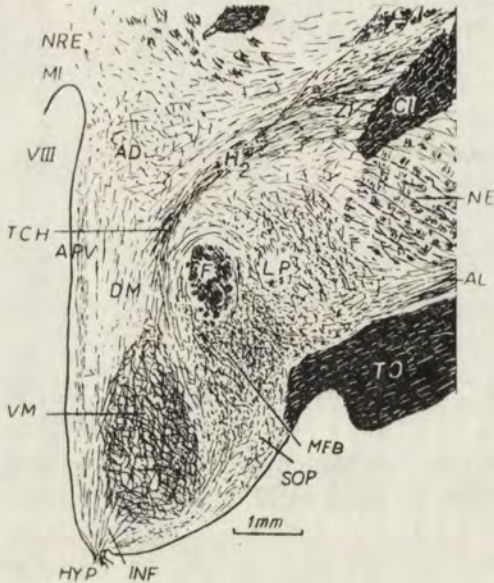


Fig. 1. Frontal section of the frontal area of the tuberal part hypothalamus of the dog. Weigert-Wolters stain

Medially, the intermediate part of the hypothalamus forms the wall of the third ventricle (Fig. 1) and dorsally it extends up to the massa intermedia of the thalamus and to the region of the subthalamus (Fig. 1 and 3). In addition, it borders upon the internal capsule, entopeduncular nucleus and lenticular ansa laterally (Fig. 1 and 3).

Ventromedial nucleus (Fig. 1, 2, 3, 11, VM)

Topography. The ventromedial nucleus is one of the large nuclei of the intermediate hypothalamus. It appears at the anterior end of the intermediate part and occupies its central portion. It has a characteristic shape in this middle portion resembling an oval (Fig. 1, VM). The ventromedial nucleus decreases in size from the middle of the intermediate part towards the rear to disappear completely at $3/4$ of its length.

Orally the ventromedial nucleus reaches the anterodorsal nucleus of the hypothalamus, from which it is separated by the fibres of the dorsal

supraoptic commissure. It is bordered by the periventricular system medially and laterally, it touches the posterior lateral nucleus and, in its caudal part the ventrolateral nucleus (Fig. 3). It is superimposed by the dorsomedial nucleus, and the infundibular nucleus lies on the its ventral side.

The length of the nucleus is about 1,7 mm in the sagittal plane and from 1 to 1,6 mm in the horizontal plane in frontal sections.

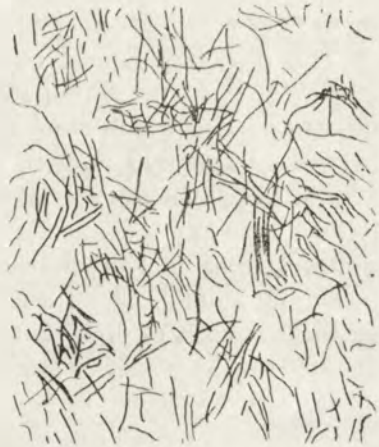


Fig. 2. Myeloarchitectonics of the ventromedial hypothalamic nucleus in the dog. Frontal section, Weigert stain

Architectonics. In Weigert sections the image of the ventromedial nucleus, composed of a dense network of wellmyelinated fibres, is very clear (Fig. 1 and 2). The network consists mainly of thin fibres which, as a rule, run in the plane of frontal sections. A lack of fibres extending in the sagittal direction is characteristic of this nucleus. The diameter of the fibres of the network ranges from 2 to 3 μ . In some series of sections the network of fibres was found denser on the lateral side of the nucleus, the main direction of fibres being the same.

Situated in the centre of the intermediate part of the dog hypothalamus the ventromedial nucleus has abundant connections (Fig. 10). The main system of fibres leaves the nucleus at the dorsal boundary (Fig. 1). It is made up of thin fibres grouped in small bundles, which reach the dorsomedial nucleus lying above the ventromedial one. Another system, not so strong as the previous one, consists of fibres which connect the ventromedial nucleus to the pituitary gland. They rise among the network of main fibres of the nucleus and turn towards the infundibulum. This connection is often overlooked by authors working in the hypothalamus (Wahren 1959, Schreiber 1963). It is impossible to establish the origin of this connection, which may indicate that it concerns the whole of the ventromedial nucleus of the dog.

The fibres of the system known as the cortico-hypothalamic tract (Wahren 1959), which connects this nucleus with some regions of the neocortex, enter the ventromedial nucleus dorsally (Fig. 1, H₂). The fibres of the tract in question run from the cortex through the internal capsule, and next through the zona incerta and the area H₂ of Forel. From the area H₂ they extend ventrally and reach the dorsal edge of the ventromedial nucleus (Fig. 1). This tract is also joined by some fibres from the entopeduncular nucleus and these fibres scatter within the ventromedial nucleus.

The posterior lateral nucleus is sited laterally to the ventromedial one (Fig. 1, LP). In addition to the fibres of the cortico-hypothalamic tract (a part of which reaches the ventromedial nucleus across the border between these two nuclei), on the boundary there is a small number of thin fibres which connect the nuclei (Fig. 1). This bundle is scanty, but it may provide a connection, directly or by means of the cells of the posterolateral nucleus, between the ventromedial nucleus and the medial forebrain bundle. The fibres of this system originate among the fibres of the network of the ventromedial nucleus and leave it in a random manner for the posterior lateral nucleus.

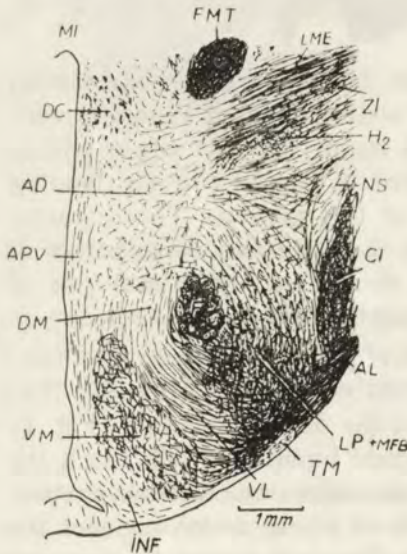


Fig. 3. Frontal section of the intermediate nuclei in the hypothalamus of the dog. The section is located about 2,5 mm posteriorly from Fig. 1. The section stained by the Weigert-Wolters method

The boundary line between the posterior lateral nucleus and the ventromedial one is very well defined. There is a clear-cut difference between these nuclei since the texture of fibres of the posterior lateral nucleus is richer and it contains many fibres which run in the sagittal

direction and belong to the medial forebrain bundle, whereas no such fibres can be seen in the ventromedial nucleus.

The fibres from the ventrolateral nucleus enter the ventromedial one on its laterocaudal side. These fibres extend laterodorsal by throughout the border area between these nuclei (Fig. 3).

The ventromedial nucleus has poor connections with the periventricular area. These connections are provided by a small number of thin fibres which run obliquely, without forming a pronounced system.

The connection of the ventromedial nucleus with the infundibular nucleus is obscure, our methods not indicating whether any fibres of the tract which runs from the ventromedial nucleus to the pituitary gland through the infundibular nucleus terminate in this last region (Fig. 3).

A large number of oval nerve cells are visible in the ventromedial nucleus in Nissl sections. They are 8—11 μ in diameter and stain poorly. The large number of nerve cells per unit area makes this nucleus easily distinguishable also in sections stained for cells, and owing to this fact it has been defined correctly in most cytoarchitectonic papers.

The ventromedial nucleus is one of the nuclei fairly early discovered of the hypothalamus. Ramon y Cajal (1904) was the first to describe it and used the name „nucleus principalis tuberis”. Since then many other authors have found this nucleus in the hypothalamus of all the mammals whose brains have been described so far, these descriptions being unanimous.

Kuhlenbeck (1954) gave a description of the ventromedial nucleus in man. Here its dimensions exceed those in the dog, being 4 mm in the sagittal plane, 3 mm vertically and 2,5 mm dorso-ventrally. In the ventromedial nucleus of man Brockhaus (1942) distinguished three parts, a magnocellular, a mediocellular and a parvocellular, on the basis of their cytoarchitectonics.

According to Diepen (1962) who based himself on the recent literature on the hypothalamus, the ventromedial nucleus is connected with the pituitary gland. The existence of these connections has now been confirmed in the dog brain. Diepen recorded also connections of this nucleus with the stria terminalis, thalamus opticus and fornix, but none of these connections has been found in the dog, although their presence here cannot be ruled out. Vallenstein and Nauta (1959) found the connections of the ventromedial nucleus with the stria terminalis in the cat.

Infundibular nucleus (Fig. 3, 10, 11, INF)

Topography. The name „infundibular nucleus” is used for a group of nerve cells situated in the ventral portion of the paraventricular system of the third ventricle. Posteriorly the infundibular nucleus is bordered

by the mammillary bodies, whereas dorsally and anterodorsally it neighbours upon the periventricular area. Dorsolaterally this nucleus is limited by the ventromedial nucleus and ventrolaterally, in its anterior part, it touches the posterior supraoptic nucleus (Fig. 1 and 3).

The dimensions of the infundibular nucleus of the dog are about 3 mm in the sagittal plane and about 600 μ in the horizontal plane in frontal sections.

Architectonics. The infundibular nucleus contains only a slight number of fibres that originate from the cells situated inside it. Most of its fibres belong to the tracts which pass through this nucleus on their way from several nuclei of the hypothalamus to the posterior part of the pituitary gland. These tracts consist of myelinated fibres, which are easily visible, especially in Weigert sections. They penetrate into the infundibulum.

Although the infundibular nucleus seems to be the ventral continuation of the periventricular area, yet it lacks the system of fibres characteristic of the periventricular system. The fibres which come from the periventricular area and reach the infundibular nucleus dorsally do not include the whole of the nucleus within their range.

A small number of poorly stained nerve cells can be seen in Nissl sections with diameters from 10 to 15 μ .

Addey and Meyer (1952) reported the presence of a connection between the infundibular nucleus and the fibres of the stria terminalis; I failed to distinguish this connection in the dog.

Mention of the infundibular nucleus can be found in different papers on the hypothalamus of all the mammals examined so far, not excluding man (Kuhlenbeck 1954). It was described as the ventral periventricular nucleus (Gurdjian 1927, Rioch 1929, 1931) or the arcuate periventricular nucleus (Kuhlenbeck 1954). Some authors of cytoarchitectonic studies on the hypothalamus describe the posterior portion of the infundibular nucleus as the premammillary nucleus. Observations of horizontal sections show that the infundibular nucleus extends as far as the mammillary bodies and there is no trace of the premammillary nucleus.

Posterior supraoptic nucleus (Fig. 1, 10, SOP)

Topography. The supraoptic nucleus of the dog consist of two parts, anterior and posterior. Only the posterior part will now be described. The posterior supraoptic nucleus is situated medially to the optic tract and is bordered by the brain floor ventrally. Dorsally, it touches the posterior lateral nucleus, whereas dorsolaterally it borders on the system of the commissura supraoptica ventralis (Meynerti).

The posterior supraoptic nucleus rises caudally to the optic chiasm. Its beginning is marked by several cells scattered among the fibres of the

ventral supraoptic commissure. Then the cells of the nucleus are shifted laterad, following the laterally extending optic tract. Here the nucleus forms a more compact cellular mass and develops remarkably, reaching 1200 μ in width and about 500 μ in height in frontal sections. These are the measurements of the posterior supraoptic nucleus in the middle portion of the intermediate part of the dog hypothalamus (Fig. 1). Somewhat further to the rear the nucleus disappears completely. At the level of its greatest expansion the posterior supraoptic nucleus touches the infundibular nucleus.

Architectonics. In the series of Weigert-Wolters sections the posterior supraoptic nucleus contains a small number of nerve fibres, because the greater part of its volume is filled with nerve cells of large size (between 20 and 30 μ in diameter).

Three systems of fibres have been found in the posterior supraoptic nucleus.

The first and most robust system of fibres reaches this nucleus from the ventral supraoptic commissure. These fibres come from the bundle of commissural fibres which is situated medially to the optic tract. They penetrate the supraoptic nucleus on the dorsolateral side and, having passed across the border, run ventromedially to disperse among the cells of this nucleus. Most of these fibres run singly and only a few of them group into bundles of no more than two fibres. The fibres of the system that comes from the ventral supraoptic commissure are well myelinated and about 5 μ in diameter.

The second system consists of fibres which approach the nucleus from the front. They are a branch from the medial forebrain bundle. The fibres of this system are less numerous than those of the first system. Within the nucleus they run oro-caudally and are well myelinated. Their diameter ranges from 3 to 4 μ .

The third system contains the smallest number of fibres. They come to the posterior supraoptic nucleus from above, from the posterior lateral nucleus, and are directed dorsoventrally.

A bundle of fibres leaves the posterior supraoptic nucleus in the ventromedial direction and, running at the bottom of the brain, it enters the infundibulum and the pituitary gland. Neurosecretory studies (Diepen 1962, Scharrer and Scharrer 1963, Schreiber 1963) showed the transmission of neurosecretory substances along this pathway. O'Connor (1948) recorded the degeneration of the supraoptic nucleus following section of the infundibulum.

A bundle of scattered fibres extends from the posterior supraoptic nucleus towards the rear and reaches the tuberomammillary nucleus,

which lies in the caudal position of the intermediate part of the dog hypothalamus.

The posterior supraoptic nuclei of both sides are connected with each other by means of some fibres of the ventral supraoptic commissure. However, this connection is not clear and should be checked by degenerative methods. It may be present in the dog, because in the guinea pig for example all the neurosecretory nuclei of both hemispheres are connected (Dankmeyer and Nauta 1945).

Not unlike the anterior supraoptic nucleus, the posterior has a large number of capillaries.

Nissl sections show the presence of large-sized nerve cells in the posterior supraoptic nucleus. These cells have a large nucleus and reach 30 μ in diameter. No multinuclear cells, described by Kuhlenbeck (1954) in the supraoptic nucleus of man, have been found.

The posterior supraoptic nucleus corresponds to the nucleus tangentialis (supraopticus) pars tuberalis of Bodian (1939) and the tuberal component of the nucleus supraopticus of Bleier (1961).

Periventricular area (Fig. 1, 3, 4, 10, 11, APV)

Topography. A thin layer of nerve cells accompanied by a characteristic system of fibres is situated under the ependymal epithelium which lines the third ventricle (Fig. 4). This is the periventricular area, which stretches for the whole length of the third ventricle in the intermediate part of the hypothalamus. It terminates in the region lying above the mammillary bodies.

The system of the periventricular area is very large and extends also under the ependymal epithelium of the third ventricle in the neighbourhood of the anterior part of the hypothalamus. Therefore, for this region I do not use the term „nucleus” which is applied to a definite area with boundaries that can be precisely defined.

In front, the periventricular area of the intermediate part of the dog hypothalamus borders on a similar system surrounding the third ventricle in the anterior part of this structure. Dorsally it reaches to the ventral nuclei of the thalamus, and in the ventral portion of the massa intermedia of the thalamus, passes to the opposite side. Laterally it touches the following nuclei of the hypothalamus (beginning at the top): The dorsal nucleus, the dorsomedial and ventromedial nuclei and (ventrally) the infundibular nucleus (Fig. 1). In the caudal portion most fibres of the periventricular area penetrate into the dorsocaudal nucleus (Fig. 3). In frontal sections the periventricular area is about 400 μ wide, the ependymal epithelium being 100 μ apart.

Architectonics. Weigert sections show a system of parallel nerve fibres which run vertically in the periventricular area. These fibres are thin and poorly myelinated (Fig. 4). Fibres from the nucleus reuniens of the thalamus and also from the external medullary lamina of that structure enter the anterior part, dorsally to this system. In the caudal part most of the fibres turn ventrocaudally and terminate in the dorsocaudal nucleus (Fig. 3).

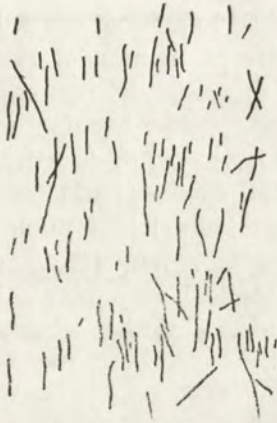


Fig. 4. Area periventricularis, myeloarchitectonics. Weigert method

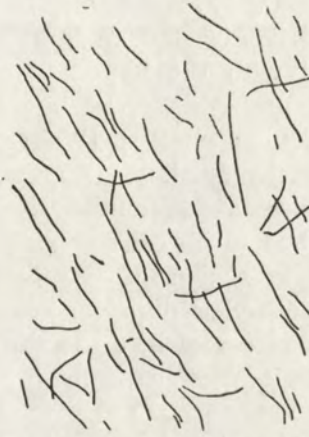


Fig. 5. Myeloarchitectonics of the ventrolateral nucleus of the hypothalamus of the dog. Weigert stain



Fig. 6. Myeloarchitectonics of the posterolateral hypothalamic nucleus. Weigert method



Fig. 7. Dorsomedial nucleus, myeloarchitectonics. Weigert stain

A small number of fibres of this system in the ventral part of the periventricular area terminate in the infundibular nucleus. This area has equally weak connections to the dorsomedial, ventromedial and dorsal nuclei. On the border between these nuclei and the periventricular area there are only a few connecting nerve fibres, which run slantingly (Fig. 3).

The periventricular area has few cells. Their measurements are about $15 \times 7 \mu$, and they stain faintly by the Nissl method.

The periventricular area has been described in most of the publications concerned with the hypothalamus of different mammals. It has been described under different but generally approximate names, e.g., the periventricular nucleus (Wahren 1959), or periventricular system of fibres (Crosby et al. 1962). Other authors, however, divide the periventricular area into a number of small nuclei. Bleier (1961) for instance, distinguished a tuberal component of the periventricular nucleus in the intermediate region of the hypothalamus. Gurdjian (1927) presented a similar complex division. From the anatomical view-point the whole periventricular region, up to the thalamus, has a similar structure, both in the anterior part and in the intermediate.

Ventrolateral nucleus (Fig. 3, 5, 11, VL)

Topography. In the posterior region of the intermediate part of the hypothalamus, the ventrolateral nucleus begins on the border between the posterior lateral nucleus and the ventromedial. At first it squeezes in between these two nuclei but farther towards the rear it develops considerably at the expense of the ventromedial nucleus, which disappears in the posterior portion of the intermediate part (Fig. 3). In frontal sections this nucleus resembles an obtuse-angled triangle in shape: one of its sides, the vertical, runs medially to the posterior lateral nucleus, another side extends dorsomedially towards the fornix, and the side which connects their ends together is nearly parallel to the wall of the third ventricle (Fig. 3).

The following hypothalamic nuclei neighbour upon the ventrolateral nucleus: the ventromedial nucleus anteromedially, the posterior lateral nucleus laterally and the dorsomedial nucleus dorsally and dorsomedially. The fornix is situated dorsolaterally to the nucleus.

Architectonics. The picture of the ventrolateral nucleus is very clear in myelin sections. It contains a uniform system of fibres (Fig. 5); this system comes from the posterior lateral nucleus, which it leaves medio-dorsally to turn dorsally having entered the ventrolateral nucleus. The fibres of this nucleus occur uniformly densely throughout the nucleus and form a wide bundle, a part of which runs out of the ventrolateral

nucleus in the dorsal direction towards the overlying dorsomedial nucleus (Fig. 3).

The cells of the ventrolateral nucleus stain poorly by the Nissl method. They are for the most part oval in shape and about $24 \times 16 \mu$ in size.

So far the ventrolateral nucleus has been distinguished in the hypothalami of few mammals, i.e., in the dog (Rioch 1931), cat (Ingram et al. 1932), Pig (*Sus scrofa*, Solnitzky 1938) and macaque (Crough 1934). In many cytoarchitectonic publications this nucleus has been confused with the ventromedial and posterior lateral nuclei, as their cells are similar in structure.

The ventrolateral nucleus is not homologous with the nuclei tuberales lateralis described in man (Wahren 1959) and in some animals. No descriptions of this nucleus in the brain of man can be found in the available literature.

Tuberomammillary nucleus (Fig. 3, 11, TM)

Topography. A flat nucleus composed of large cells lies ventral to the posterior lateral nucleus in the caudal portion of the intermediate part. It is called the tuberomammillary nucleus, because it begins in the intermediate (tuberal) part of the hypothalamus and reaches as far as the mammillary bodies, where it terminates laterally to the lateral mammillary nucleus. The close neighbourhood of the tuberomammillary nucleus upon the posterior supraoptic nucleus can be observed in horizontal sections. The anterior portion of the former is situated hardly several millimetres behind the latter. Dorsally, the tuberomammillary nucleus borders on the posterior lateral and ventrally, it touches the floor of the brain.

Architectonics. The main system of fibres of the tuberomammillary nucleus consists of those from the medial forebrain bundle. Along with them a few fibres from the posterior supraoptic nucleus approach the tuberomammillary nucleus. This system enters the nucleus from the front to scatter among the cells. Within the nucleus there is also another system of thicker fibres which take origin in this region, turn mediocaudally in the caudal portion of the nucleus and reach the lateral mammillary nucleus, where they terminate (Fig. 3).

The cells of the tuberomammillary nucleus belong to the largest in the dog hypothalamus. Their measurements fluctuate from 25 to 35 μ in diameter in round cells, but there are occasional oval cells in which they amount to about 18 by 35 μ .

This nucleus is often mentioned in different cyto- and myeloarchitectonic descriptions of the hypothalamus. The nomenclature of this nucleus is various. Kuhlenbeck (1954) describes it as the lateral mammillary

nucleus, whereas Gurdjian (1927) and Rioch (1931) include it in the lateral area of the hypothalamus. Only in Morgan's (1930) publication are the topography and the name of this nucleus in the dog identical.

Posterior lateral nucleus (Fig. 1, 3, 6, 10, 11, LP)

Topography. The lateral area of the dog hypothalamus has been divided into two nuclei, the anterior lateral (Śmiałowski 1966) and the posterior lateral. The posterior lateral nucleus of the dog hypothalamus is situated on the lateral side of the intermediate part.

The posterior lateral nucleus borders on the anterior lateral orally and ends at the level of the anterior part of the mammillary bodies in frontal sections. Dorsally the posterior lateral nucleus reaches to Forel's area H_2 (Fig. 1); ventrally, it borders successively on the posterior supra-optic nucleus and the optic tract (Fig. 1), and caudally touches the tubero-mammillary nucleus and the floor of the brain (Fig. 3). Similarly, the posterior lateral nucleus has a large number of neighbours on the medial side. These are (beginning at the top) the dorsomedial, ventrolateral and ventromedial nuclei (Fig. 3). The boundary between the posterior lateral nucleus and the internal capsule on the lateral side is hard to distinguish. It may be defined precisely only in silver sections, for here the non-myelinated fibres, which occur in the posterior lateral nucleus and are absent from the internal capsule, also stain. In the caudal portion of the nucleus the ventromedially descending fibres of the internal capsule reduce remarkably the area occupied by the lateral nucleus. The posterior lateral nucleus disappears completely where the mammillary bodies turn up.

The medial boundary of the posterior lateral nucleus is marked out for a long distance by the fibres of the cortico-hypothalamic tract. They run dorsoventrally on the border of the posterior lateral nucleus with the dorsomedial and ventromedial nuclei (Fig. 1).

Architectonics. The myeloarchitectonic picture of the posterior lateral nucleus, which is the largest nucleus in volume in the intermediate part of the dog hypothalamus, is very complex. Many systems of fibres run across this nucleus or terminate in it, crossing each other throughout its area.

The main system, which occurs in both parts of the lateral nucleus, consists of fibres of the medial forebrain bundle; they arise in the olfactory region of the telencephalon and in the septum (Zyo et al. 1963), and run orocaudally, perpendicularly to the plane of frontal sections. They scatter, as a rule, all over the area of the lateral nucleus, but most of them lie on the ventrolateral side of the fornix (Fig. 1). Many fibres of the medial forebrain bundle end in the posterior lateral nucleus and

only a small number of them reach the posterior supraoptic and tubero-mammillary nuclei. In the caudal portion of the nucleus of the fibres cross its boundary and extend as far as the ventral region of the mesencephalic tegmentum. The medial forebrain bundle has connections with septum, the lateral preoptic area, the lower olfactory regions, the amygdaloid complex and also with the neocortex. Its course is easily seen, especially in horizontal sections.

Another system which scatters in the posterior lateral nucleus is that of the fibres from the lenticular ansa (Fig. 3). They run lateroventrally into the area of the nucleus from the lateral side and then separate to extend dorsally and medially. In frontal sections they are plainly visible as well myelinated nerve fibres which pass from the front slightly backwards. This pathway runs beneath the entopeduncular nucleus and conducts impulses from the globus pallidus (Fig. 3).

The third system is composed of fibres of the cortico-hypothalamic tract. This pathway extends from the neocortical region through the internal capsule to Forel's area H_2 and thence as a compact bundle farther ventrally to reach the dorsomedial margin of the posterior lateral nucleus. At various levels of the posterior lateral nucleus some fibres of this tract turn laterad and disperse (Fig. 1).

In the caudal portion of the lateral nucleus the fibres of the hypothalamo-tegmental tract run parallel to the system of cortico-hypothalamic fibres. They leave the lateral nucleus at its medial and, partly, dorsal boundary, turn dorsad and arrive in Forel's area H_2 , where they bend caudally and extend up to the tegmentum.

The posterior lateral nucleus receives a rich system of fibres from the ventrolateral nucleus. This system approaches the caudal part of the nucleus. It is well developed and passes throughout the border area of these two nuclei (Fig. 3). Entering the posterior lateral nucleus it is directed lateroventrally and it terminates in the ventral region of this nucleus.

There is a poor connection between the posterior lateral nucleus and the ventromedial. On the border of these nuclei there occur some fibres of the cortico-hypothalamic tract, which are not very numerous in this region, and besides them some thin nerve fibres slant from the posterior lateral nucleus to the ventromedial (Fig. 1).

The fornix which extends dorsally to the posterior lateral nucleus, sends out fine fibres over its whole course in this region. They next penetrate into the lateral nucleus. Having left the fornix they bend oroventrad and next vanish amidst the essential system of fibres of the nucleus (Fig. 1). This connection has been confirmed by degenerative

studies of Vallenstein and Nauta (1959). In the dog hypothalamus the fibres of this system have been observed only in the ventral portion of the fornix.

A few fibres which belong to the dorsal supraoptic commissure also run through the posterior lateral nucleus. They extend laterodorsally as single scattered, fibres towards the subthalamus.

The posterior lateral nucleus shows a strong connection with the amygdaloid complex. This connection is obtained by the medium of two pathways. The first of them leads from the amygdaloid complex to the substantia innominata Reicherti, where it turns mediad and then medio-caudad and mingles with the fibres of the medial forebrain bundle. With this last it reaches the lateral nucleus. The other connection is much shorter. Its fibres leave the central and medial nuclei of the amygdaloid complex laterally and passing close to the optic tract, mingle with the fibres of the lenticular ansa, and together with a majority of these fibres, terminate in the lateral nucleus of the hypothalamus (Fig. 1).

No data concerning a connection of the lateral nucleus with the pituitary gland have been found in the literature available. A connection of this kind has not been detected by anatomical methods in the dog brain, either.

The lateral nucleus contains a small number of nerve cells. It is, above all, a place where a large number of nerve fibres pass. The cells that can be seen in this nucleus are oval in shape and about $12\ \mu$ in diameter. There are also triangular cells, the height of which does not exceed $12\ \mu$. They stain well by the Nissl method.

The posterior lateral nucleus has been described in the hypothalamus of all the mammals worked out so far and also in lower vertebrates, in which it is often called „the bed nucleus of the medial forebrain bundle” (Ban 1964). Only Diepen (1962) does not treat the lateral nucleus as a distinct nucleus in the hypothalamus in man. The connections of the lateral nucleus are unusually rich. In addition to those described above, the degenerative studies of Maršala (1963) showed a connection of the lateral nucleus with the motor, premotor and prefrontal cortex in the cat. Most fibres of this tract run along with the internal capsule (in its ventral part). According to Maršala (1963), only fibres from the medial prefrontal cortex come via the septum and the medial forebrain bundle. Besides, the studies of Zyo et al. (1963) carried out by the degenerative method demonstrated the connection of the lateral nucleus with the gyrus cinguli and stria Lancisii in the rabbit. This pathway traverses the septum and the preoptic area and terminates in the posterior lateral nucleus as one of the components of the medial forebrain bundle.

Dorsomedial nucleus (Fig. 1, 3, 7, 10, 11, DM)

Topography. The dorsomedial nucleus is one of the smallest nuclei of the intermediate part of the dog hypothalamus. Situated above the ventromedial nucleus, it is nearly rectangular in frontal sections. The sides of this rectangle are 1 and 2 mm long and it is oriented with its longer side upwards. The dorsomedial nucleus neighbours also on the periventricular area medially, on the dorsal nucleus dorsally, and laterally on the fornix (from which it is separated by a bundle of fibres of the cortico-hypothalamic tract and the hypothalamo-tegmental tract running from Forel's area H_2). In its caudal portion, where the fornix comes downwards, the nucleus borders for a small distance on the dorsal portion of the posterior lateral nucleus. Its caudal boundary is defined by the ventrolateral nucleus, which develops caudally behind the dorsomedial.

Architectonics. In Weigert sections the dorsomedial nucleus contains a characteristic system of parallel dorsoventral fine fibres (Fig. 1 and 7). They are grouped into bundles of 2 or 3 fibres each and run right across the nucleus, nearly parallel to each other. This system seems to be extension of the fibres which leave the ventromedial nucleus and it enters the dorsomedial at its ventral boundary (Fig. 1).

Fibres from the cortico-hypothalamic tract, which run dorso-ventrally near the lateral boundary of the dorsomedial nucleus, enter it across this boundary (Fig. 1). Entering the nucleus they change their direction to ventromedial and are easy to distinguish, being nearly twice as thick as the fibres of the main system of the nucleus. The dorsolateral region of the nucleus receives fibres from the dorsal portion of the posterior lateral nucleus. They extend lateromedially and enter the nucleus at its lateral boundary.

A poor system of fibres from the dorsal nucleus approaches the dorso-medial from the dorsal side (Fig. 3). This system is composed of fibres, which run in a random manner.

On the ventrocaudal side the dorsomedial nucleus receives a connection from the ventrolateral. It consists of fibres which leave the ventrolateral nucleus in the dorsal direction (Fig. 3).

The dorsomedial nucleus described by other authors does not correspond exactly to the present description of this nucleus in the dog. The dorsomedial nucleus of Rioch (1929) is homologous with the nucleus described as dorsal in this paper, whereas the dorsomedial nucleus of Diepen (1962) corresponds to the dorsal portion of the periventricular area in my division.

Dorsal nucleus (Fig. 1, 3, 8, 10, 11, AD)

Topography. The dorsal nucleus is an area occupying the dorsal portion of the dog hypothalamus, in which portion it has the most lateral position.

Dorsally, it reaches up to the ventral nuclei of the thalamus (Fig. 1). Medially it borders for its whole course on the periventricular system of the third ventricle, and laterally it is limited by the zona incerta and Forel's area H₂. Caudally, this nucleus develops and combines with the periventricular system into the dorsocaudal nucleus, which is the furthest caudal nucleus of the dog hypothalamus (Fig. 3).



Fig. 8. Dorsal nucleus, myeloarchitectonics, Weigert stain



Fig. 9. Dorsocaudal nucleus, myeloarchitectonics, Weigert stain

Architectonics. Weigert sections show a system of fibres which form a loose network in this nucleus (Fig. 8). This network is composed of fibres which pass through the dorsal nucleus in different directions.

The main system of fibres coming out of the dorsal nucleus runs to the zona incerta and the hypothalamo-tegmental tract. This system arises among the fibres of the network and passes across the lateral boundary of the nucleus (Fig. 1, 8, 10).

Several fibres of the system of the external medullary lamina of the thalamus reach this nucleus dorsally. These fibres are fairly thick (3–4 μ in diameter) and easy to find (Fig. 1).

Medial to the dorsal nucleus is the periventricular area. These two regions are poorly connected. A few single fibres run between them obliquely or horizontally. The dorsal nucleus has a similarly faint connection with the dorsomedial nucleus, lying on its ventral side.

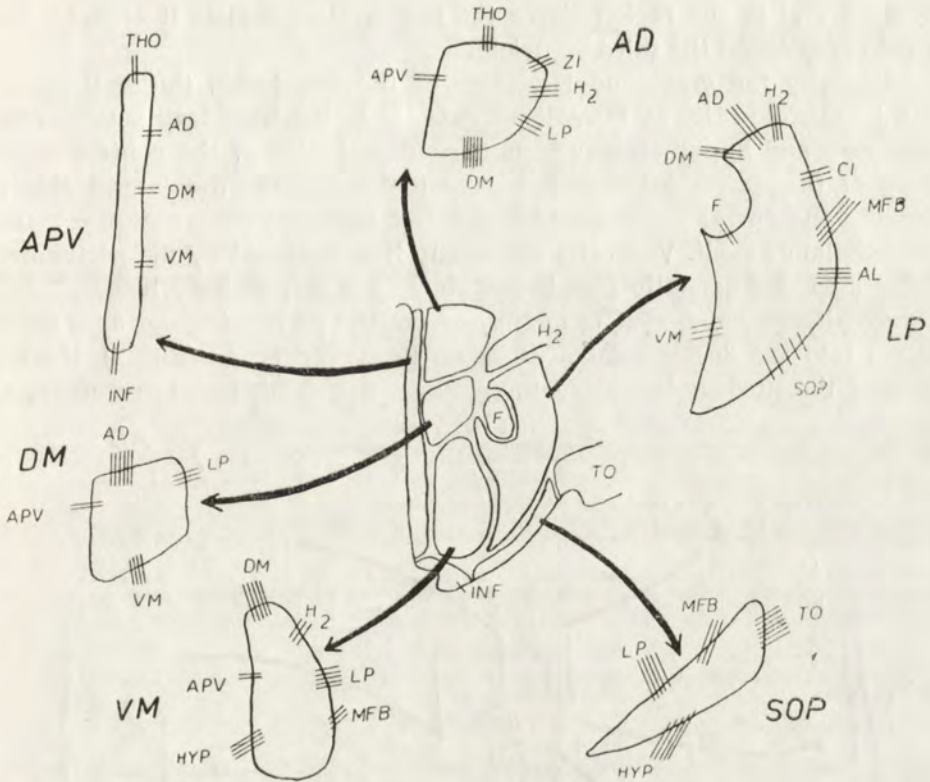


Fig. 10. A diagram of connections of nuclei in the intermediate part of the hypothalamus in the dog. Shaded spots denote the direction and density of fibres in particular systems. The diagram plane corresponds with Fig. 1

Caudoventrally, the dorsal area is bordered by the ventrolateral nucleus, from which it receives some fibres at the rear. These fibres run medially to the fornix in the dorsal direction and come into the dorsal nucleus on the ventrolateral side (Fig. 3).

Many authors (Kuhlenbeck 1954, Diepen 1962, Westwood 1962) use the term „area dorsalis” for this nucleus, but as this area has distinct boundaries, I think the name dorsal nucleus is more appropriate.

Dorsocaudal nucleus (Fig. 3, 9, 11, DC)

Topography. This nucleus appears in the posterior portion of the intermediate part. In frontal sections it lies at the side of the ventral diencephalic sulcus. In this nucleus the fibres of the periventricular system (periventricular area) join the system of fibres coming from the thalamus and the dorsal nucleus (Fig. 3). The nucleus begins in the central portion of the intermediate part. Further to the rear it develops remarkably

ventrad and in the region above the mammillary bodies it occupies the whole area round the third ventricle.

Medially the dorsocaudal nucleus of the dog forms the wall of the third ventricle (Fig. 3). Dorsally it extends to the boundary between the thalamus and hypothalamus (running at the height of the ventral boundary of the massa intermedia of the thalamus). On the lateral side it touches the dorsal nucleus and somewhat further to the rear the mammillothalamic tract. Ventrally and orally it is bordered by the periventricular area and caudally terminates above the mammillary bodies.

Architectonics. A system of fibres from the periventricular area penetrates into the dorsocaudal nucleus on the ventral side (Fig. 3). Having crossed the nuclear boundary these fibres run caudad and are arranged

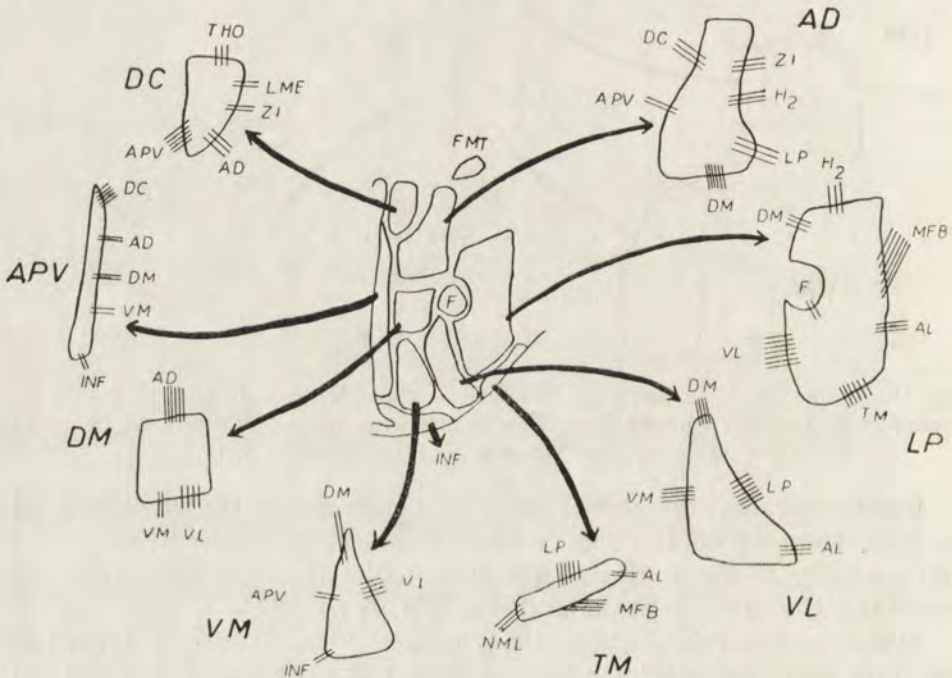


Fig. 11. A diagram of connections of the intermediate (tuberal) nuclei in the hypothalamus of the dog. The diagram plane corresponds with Fig. 3

perpendicularly to the frontal plane. This is the course of the first system; the second is composed of thicker fibres, coming from the nucleus reuniens of the thalamus and directed dorsocaudally.

There is still another system of fibres entering the dorsocaudal nucleus from the lateral side (Fig. 3). It is a dispersed tract which takes origin from the zona incerta, the cortico-hypothalamic tract, the lenticular ansa,

the entopeduncular nucleus, the internal capsule and probably the caudate nucleus.

The picture of the dorsocaudal nucleus provided by Nissl sections resembles that of the other nuclei of the hypothalamus.

The caudal portion of this nucleus sends out a bundle of well-myelinated fibres, which according to Ban (1964), reaches the ventral region of the tegmentum as the dorsal longitudinal fascicle. This nucleus has been described in many animals as the dorsocaudal area (Diepen 1962), the dorsal area (Bleier 1961) or the posterior periventricular nucleus (Rioch 1929, 1931).

DISCUSSION

Most hypothalamic nuclei described previously in other mammals have been found in the intermediate part of the dog hypothalamus at present. Architectonic analyses of particular nuclei have been discussed above and a table has been constructed to juxtapose the most commonly used names of these nuclei, only the problems connected with the occurrence of some controversial areas will be discussed now.

The dog lacks the nucleus tuberis lateralis and hence this has not been described here. The description of this nucleus in Morgan's paper (1930) is erroneous, because the author has based himself only on the analysis of cells of the dog hypothalamus. Bleier (1961) describes the area of the tuber cinereum in the ventral portion of the intermediate part of the cat. According to Diepen (1962), the nucleus tuberis lateralis occurs in man and in the Primates. Diepen et al. (1956) found the nucleus tuberis lateralis in the elephant (*Loxodonta africana* Blum). In the hypothalamus of the dog the area in which this nucleus might be situated is occupied by the posterior lateral and ventromedial nuclei. These nuclei extend as far as the floor of the brain in the dog.

Another nucleus that has not been found in the dog is the nucleus supraopticus diffusus. Mentioned in the hypothalamus of man in Kuhlénbeck's (1954) paper, it has not been confirmed by Diepen (1962). According to Kuhlénbeck, it includes a group of cells which make up an interstitial nucleus among the fibres of the supraoptic commissures. Rioch (1929, 1931), too, observes it in the hypothalamus of Carnivora. According to him, in the dog this nucleus forms a bed nucleus of the supraoptic commissures and is situated among their fibres. On the other hand, Bleier, who based herself on cytoarchitectonic studies, did not describe the nucleus supraopticus diffusus in the brain of the cat. In the dog myelocarchitectonic analysis also did not provide sufficient evidence to distinguish this nucleus. The descriptions of the diffuse supraopticus

Table I

Identification of the nuclei of the pars tuberalis (intermedia) hypothalami of the dog

Craigie 1925 rat	ventro- medialis	Gurdjian 1927 rat	ventro- medialis	Kuhlenbeck 1954 man	ventro- medialis	Wahren 1959 man	ventro- medialis	Bleier 1961 cat	ventro- medialis	Westwood 1962 ferret	ventro- medialis	Diepen 1962 man	ventro- medialis	Ban 1964 rabbit	ventro- medialis	Śmiałowski 1966 dog	ventro- medialis
dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis	dorso- medialis
n. poste- rior	xxx	area dorsalis	dorso- medialis	dorso- medialis	n. dorsalis	n. dorsalis	n. dorsalis	posterior area	dorso- medialis	dorsal area	area dorsalis	area dorsalis	area dorsalis	dorso- medialis	n. dorsalis	n. dorsalis	n. dorsalis
n. poste- rior	n. poste- rior	n. poste- rior	n. poste- rior	n. poste- rior	xxx	xxx	xxx	dorsal area	dorsal area	xxx	area dorso- caudalis	area dorso- caudalis	n. posterior	n. posterior	n. dorso- caudalis	n. dorso- caudalis	n. dorso- caudalis
xxx	n. peri- ventricula- ris post.	periventri- cularis post.	periventri- cular fibers	periventri- cular fibers	n. periven- tricularis	n. periven- tricularis	n. periven- tricularis	n. periven- tricularis, tuberal comp.	periventri- cularis post.	periventri- cularis post.	xxx	xxx	stratum peri- ventriculare	stratum peri- ventriculare	area peri- ventricula- ris	area peri- ventricula- ris	area peri- ventricula- ris
arcuatus	n. periv. post. pars ventralis	periventri- cularis post. pars ventr.	periventri- cularis ; rcuatus	periventri- cularis ; rcuatus	infundibu- laris	infundibu- laris	infundibu- laris	infundibu- laris	periventri- cularis arcuatus	periventri- cularis arcuatus	infundibu- laris	infundibu- laris	arcuatus	arcuatus	infundibu- laris	infundibu- laris	infundibu- laris
n. supra- opticus	tangentia- lis	tangentialis	supraopticus+	supraopticus+	supraopticus	supraopticus	supraopticus	supraopticus tuberal comp.	supraopticus caudal div.	supraopticus caudal div.	supraopticus	supraopticus	supraopticus	supraopticus	supraopticus	supraopticus	supraopticus
xxx	xxx	ventro- lateralis	xxx	xxx	xxx	xxx	xxx	tuber cin. area	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx	xxx
area lateralis	n. lateralis	lateral area	n. lateralis	n. lateralis	n. lateralis	n. lateralis	n. lateralis	lateral area	lateral area	lateral area	lateral area	lateral area	area lateralis	area lateralis	n. lateralis	n. lateralis	n. lateralis
n. mamill. lat.	n. mamill. lat.	xxx	xxx	xxx	tubero- mamill.	tubero- mamill.	tubero- mamill.	tubero- mamill.	tubero- mamill.	xxx	xxx	tubero- mamill.	xxx	xxx	n. tuberoma- miliaris	n. tuberoma- miliaris	n. tuberoma- miliaris
xxx	xxx	n. tuberis	n. tuberis	n. tuberis	tuberis later	tuberis later	tuberis later	tuber cin. area	xxx	xxx	xxx	n. tuberis lat.	xxx	xxx	xxx	xxx	xxx
xxx	xxx	perifor- nicalis	perifor- nicalis	perifor- nicalis	perifor- nicalis	perifor- nicalis	perifor- nicalis	xxx	xxx	xxx	xxx	perifor- nicalis	xxx	xxx	xxx	xxx	xxx

nucleus probably took origin from the fact that in the rostroventral portion the cells of the posterior supraoptic nucleus are scattered among the fibres of the ventral supraoptic commissure (of Meynert). They undoubtedly belong to the posterior supraoptic nucleus in the dog.

The third nucleus indistinguishable in the dog brain is the area described by Bleier (1961) as the tuber cinereum in the cat hypothalamus. According to Bleier this area surrounds the ventromedial nucleus with a ring of its cells. No such nucleus occurs in the dog and its presence in the hypothalamus in the cat is questionable. Bleier distinguished this nucleus on the basis of a cytoarchitectonic analysis, which on account of the great similarity of the cells in the ventral region of the intermediate part of the hypothalamus may cause some gross errors in the description.

The further two nuclei that I failed to find in the hypothalamus of the dog are the perifornical and intrafornical nuclei described by Solnitzky (1939) in the pig (*Sus scrofa*). According to Solnitzky, who was the only author to describe the intrafornical nucleus, it consists of several cells sited among the bundles of fornical fibres. The perifornical nucleus was described more frequently (Diepen 1962, Gurdjian 1927). According to Solnitzky, it is composed of a layer of cells which surround the fornix for its whole length in the hypothalamus, from the anterior part to the mammillary bodies. In *Sus scrofa* this nucleus consists of a layer of 4—8 nerve cells. Rioch (1929) described a similar nucleus in the dog. These authors applied exclusively cytoarchitectonic criteria. My observations show that there are some nerve cells in the vicinity of the fornix in the dog, but they belong directly to the nuclei which border on the fornix. Myelin sections reveal no other structure of fibres close to the fornix, which would justify the distinction of the perifornical nucleus and, therefore, it has not been described here as a distinct nucleus of the hypothalamus.

Out of the nuclei described in the present paper special attention should be given to the ventrolateral nucleus, so far distinguished merely in the dog's hypothalamus (Rioch 1931), cat (Ingram et al. 1932), macaque (Crcugh 1934) and pig (Solnitzky 1939). It was not mentioned at all in other available papers. It is probably so, because Nissl sections provide no criteria for the distinction of this nucleus. The ventrolateral nucleus is evident in myelin sections.

SUMMARY

This paper describes the topography and connections of nuclei of the intermediate part in the dog's hypothalamus, based mainly on a series

of myelin sections from the brain of the dog, stained by the Weigert-Wolters method.

The intermediate part of the hypothalamus is situated between the anterior part of this structure frontally and the mammillary bodies caudally.

The following areas have been described in the intermediate part: the ventrolateral, dorsomedial, dorsocaudal, dorsal, infundibular, posterior lateral, posterior supraoptic, ventrolateral and tuberomammillary nuclei as well as the periventricular area. These areas were distinguished in the hypothalamus of most other animals with the exception of the ventrolateral nucleus, which was reported only from a few mammals.

In general, the myeloarchitectonic analysis of the intermediate part of the hypothalamus of the dog showed that this region does not differ much from the essential structural scheme of the hypothalamus in other animals in topography, structure and connections, through a few nuclei distinguished by some authors, such as the nucleus tuberis lateralis, nucleus supraopticus diffusus, the area of the tuber cinereum and the perifornical and intraforncial nuclei could not be found in the dog.

ABBREVIATIONS

AD	dorsal nucleus	MFB	medial forebrain bundle
AL	ansa lenticularis	MI	massa intermedia thalami
APV	periventricular area	NE	nucleus entopeduncularis
CI	capsula interna	NML	nucleus mammillaris lateralis
CSOD	commissura supraoptica dorsalis	NRE	nucleus reuniens thalami
CSOV	commissura supraoptica ventralis	NS	nucleus subthalamicus
DC	nucleus dorso-caudalis	SOP	nucleus supraopticus posterior
DM	nucleus dorso-medialis	TCH	tractus cortico-hypothalamicus
F	fornix	THO	thalamus opticus
FMT	fasciculus mamillo-thalamicus	TM	nucleus tubero-mammillaris
H ₂	campus H ₂ Foreli	TO	tractus opticus
HYP	tractus hypothalamo-hypophysealis	VL	nucleus ventro-lateralis
INF	nucleus infundibularis	VM	nucleus ventro-medialis
LME	lamina medullaris externa thalami	V III	ventriculus tertius (third ventricle)
LP	nucleus lateralis posterior	ZI	zona incerta

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Book review

Nervous and Hormonal Mechanisms of Integration. Symposia of the Society for Experimental Biology, XX, ed.: G. M. Hughes; Univ. Press, Cambridge 1966, VIII + 565 pages, 213 figures, 22 plates, an Author Index and Subject Index.

The Society for Experimental Biology has organized its annual symposia in Great Britain since the end of the second World War. The themes range from biochemistry to animal behavior. The proceedings of these meetings are published yearly in separate volumes and each issue is eagerly expected by biologists all over the world.

In September, 1965, the twentieth symposium of the Society took place in St. Andrews, Scotland, conjointly with the American Society of Zoologists. The Symposium was meant to follow up the fourth Symposium held in 1949, and published in 1950, on physiological mechanisms in animal behaviour; in the latter, Professor J. Konorski delivered his talk on the mechanisms of learning, where he developed his ideas on the nervous plasticity.

The recent, 20th volume contains a series of papers which we can subdivide into several groups. Thus, M. A. Sleigh (Bristol) spoke on the coordination and control of cilia, he investigated mainly protozoan cilia, but discussed also problems of ciliary epithelia. R. K. Josephson delivered a paper on mechanisms of integration in coelenterates; T. Sibaoka (Sendai, Japan) gave a brilliant talk on action potentials in plant organs.

Apart of these papers concerning rather discrete and dispersed fields of biology, there was a group of papers concerned with integration in crustacea: D. Kennedy, W. H. Evoy and H. L. Fields (Stanford Univ.) discussed the neuronal basis of crustacean reflexes; D. M. Maynard (Michigan) spoke on integration in crustacean ganglia; C. A. G. Wiersma (Pasadena) reported on his experiments concerning crustacean visual pathway; G. A. Horridge (St. Andrews) discussed the optikinetik response in these animals. Closely related to the theme of integration were the papers on the mechanisms subserving rhythmic behavior in Arthropods, by D. M. Wilson (Berkeley) and on the coordination of walking movements in Arthropods, by G. Wandler (Max-Planck-Institut, Seewiesen).

Two papers discussed the sense physiology in insects: K. D. Roeder's and R. S. Payne's (Medford, Mass.) on acoustic orientation of a moth in flight and of D. Schneider's (Seewiesen) on the chemical sense communication in insects.

There was a group of reports on transmitters and neurosecretion: chemical transmitters in invertebrate nervous systems by H. M. Gerschenfeld (Buenos Aires) and production of hormones by neurones and the role of neurosecretion by H. A. Bern (Berkeley).

Three talks concerned the reproductive behavior: W. Loher and F. Huber (Tübingen and Köln) spoke on the nervous and endocrine control of sexual behavior in the grasshopper; R. A. Hinde and E. Steel (Cambridge) reported on integration of reproductive behavior of female canaries, and B. Baggerman (Groningen, Netherlands) discussed the endocrine control of reproductive behavior in the Stickleback.

Finally, four speakers concerned themselves with the experimental approach to the problems of nervous plasticity in several different groups of animals; R. B. Clark (Bristol) spoke on the integrative action of a worm's brain, including the neurosecretion, regeneration innate behavior, habituation and learning; J. Bruner (Paris) discussed his and L. Tauc's results on the long-lasting phenomena in the molluscan nervous system, related to the habituation and conditioning processes on the neuronal level; M. J. Wells (Cambridge) who depicted the history and the present state of investigations into the learning in the octopus; and, finally, W. Kozak, who delivered a talk on the basic patterns of plastic change in the mammalian nervous system, based on his experiments made together with R. Westerman, J. Bruner and E. Jankowska.

Włodzimierz Kozak, Warsaw, Poland

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