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CONTENTS — VOL. XXII

NO. 1

NO. 2

NO. 3

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No. 1

NOTICE

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SOME PROPERTIES OF CONDITIONED INHIBITION

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Conditioned inhibition *sensu stricto* is a kind of internal inhibition, produced when a compound composed of an extra stimulus (called conditioned inhibitor) and a positive conditioned stimulus is applied without reinforcement and, in consequence, acquires inhibitory properties. Investigations on this sort of inhibition were very extensive, particularly in the first two decades of this century (K r z h y s h k o v s k i j 1909, L e p o r s k i j 1911, C h e b o t a r e v a 1912, D e g t i a r e v a 1914, and others) and many interesting properties of it were found. On the basis of these studies K o n o r s k i (1948) proposed the following interpretation of conditioned inhibition: in the inhibitory compound composed of the conditioned inhibitor (S_0) and the conditioned stimulus (S_1) the stimulus S_0 acquires strong inhibitory properties; on the other hand, stimulus S_1, which has been repeatedly applied alone with reinforcement, preserves its excitatory features only slightly contaminated by inhibition produced by the occasional non-reinforcement of this stimulus when applied in compound with S_0. In other words, whereas the centre of S_0 forms purely inhibitory connections with the centre of the unconditioned stimulus, the centre of S_1 is connected with the unconditioned centre chiefly by facilitatory connections. And thus, the inhibitory effect of the compound $S_0 S_1$ would result from the balance between inhibitory and excitatory impulses impinging upon the unconditioned centre. K o n o r s k i has shown that all the known properties of conditioned inhibition might be easily explained by such a scheme (cf. K o n o r s k i 1948, p. 154).

The crucial experiment devised to verify this hypothesis is the following one: If after the establishment of the inhibitory reflex to

the compound S_0S_1, we cease to apply stimulus S_1 alone, and apply it only in compound S_0S_1 without reinforcement, then the positive reflex to stimulus S_1 should be extinguished. In consequence, when after a series of such trials, stimulus S_1 alone is applied again, it should produce an inhibitory effect, as if it were applied alone without reinforcement.

Experiments somewhat similar to those devised above were performed long ago by Degtiareva (1914) in Pavlov's laboratory. After establishing conditioned inhibition to the compound S_0S_1 she applied this compound four times in succession; then she repeatedly applied stimulus S_1 alone without reinforcement to test its resistance to extinction. She found that the positive effect of stimulus S_1 was fully preserved and its acute extinction occurred at the same time as extinction of this stimulus when the compound S_0S_1 had not been applied previously. However, these experiments were not quite conclusive, since fourfold application of the compound S_0S_1 might have been insufficient to produce extinction of the stimulus S_1. Besides, it must be taken into account that this author applied the conditioned inhibitor and the conditioned stimulus in overlapping sequence, and therefore such a compound might be perceived by the animal as a stimulus different from stimulus S_1.

Therefore, it seemed necessary to reinvestigate this problem in detail taking the following precautions: 1^0, to use chronic and not acute extinction of the stimuli, because acute extinction does not give a true picture of the development of the inhibitory process (cf. Konorski 1948, p. 183, Konorski and Szwejkowska 1950); 2^0, to avoid the masking of physical features of the conditioned stimulus in the inhibitory compound. To satisfy this last condition the two stimuli forming the compound, S_0 and S_1, were always applied *in sequence*, so that S_0 had been discontinued before the application of S_1. These precautions helped to obtain clearcut results.

MATERIAL AND METHODS

The experiments were performed on 9 dogs in the regular sound-proof conditioned reflex chamber. In all dogs alimentary conditioned reflexes were used; in two animals the classical (type I) conditioned reflexes, in the others instrumental conditioned reflexes (type II) were trained.

In classical conditioned reflexes the reinforcement followed the conditioned stimulus after 20 seconds. Intertrial intervals lasted 4—5 minutes. Salivation was recorded by the Ganike—Kupalov method modified in a way to reduce the amount of air between the water system and the scale.

Instrumental reflexes were elaborated by Konorski and Miller's tech-

nicque (1933). The instrumental response consisted in placing the right foreleg on the foodtray. Reinforcement followed immediately the motor response. Intertrial intervalls were 1—3 minutes.

When the positive conditioned reflexes to a number of stimuli (according to the schedule of the given experiment) had been firmly established, the inhibitory compound was introduced. In this compound the conditioned stimulus was always applied after the sessation of the conditioned inhibitor, either immediately, or folllowing an interval of 5 seconds. Such procedure was introduced in order to avoid posssibility that the sound of the conditioned stimulus would be masked by the sound of the conditioned inhibitor.

<center>RESULTS</center>

<center>I</center>

In two dogs, Nos. 1 and 2, alimentary conditioned reflexes were esttablished to a metronome and to the sound of bubbling of water. Wlhen these reflexes had been firmly established a new stimulus, whistle, was introduced and applied for 10 seconds before the application of the metronome, which lasted 20 seconds and was not reinforced by food. This compound was applied once daily among the positive stiimuli (the metronome alone and bubbling) applied with reinforcement.

In the course of training the salivary reaction to the metronome preceded by the whistle gradually diminished. In dog No. 1 it dropped to 0-12 grades of the scale, while the reaction of the metronome applied aloone amounted to 30-50 grades; in dog No. 2 the reaction to the inhibitory compound was 0-15 grades, while to the positive stimulus it was 20-40 grades.

After about 50 applications of the inhibitory compound a new series of experiments began in which the inhibitory compound continued to be applied once a day, whereas the application of the metronome alone was discontinued, and so the compound whistle-metronome was applied among the applications of bubbling only.

The inhibitory compound was applied in such manner about 40 times; according to the data of K o n o r s k i and S z w e j k o w s k a (1950) thiis number of unreinforced trials is quite sufficient to extinguish the comditioned reflex. After this period the effect of the metronome applied aloone was tested. In each dog it elicited a salivary reaction of 40 grades ancd the general positive motor reaction towards the foodtray was quite eviident. Thus, there was no extinction of the reflex to the conditioned stiimulus alone in spite of its numerous applications without reinforcement as a part of the inhibitory compound. The course of these experiments is presented in Fig. 1.
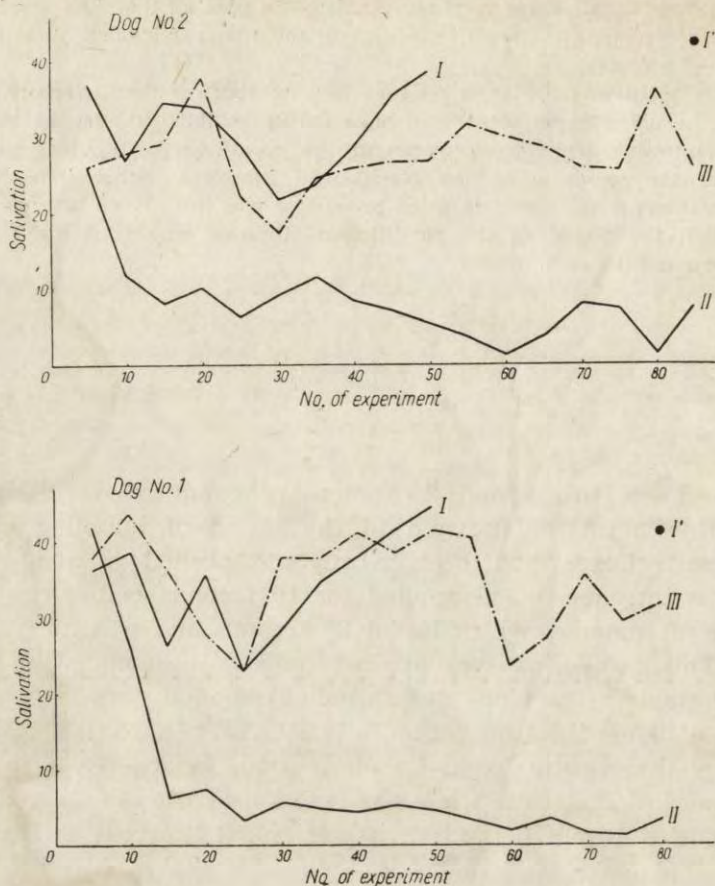
Fig. 1. Course of experiments with salivary conditioned reflexes.

Abscissae — experimental days. Ordinates — salivation to conditioned stimuli in grades of the manometer. Each point of the curves shows the average of five successive experiments. Curve I — salivation to stimulus S_1 applied separately. Curve II — salivation to stimulus S_1 applied in compound with S_0. Curve III — salivation to stimulus S_2. Point I' — salivation to stimulus S_1 applied after a period of exclusive application of S_0S_1.

II

In two dogs, Nos. 3 and 4, similar experhments were performed with instrumental conditioned reflexes.

Dog No. 3. Positive conditioned reflexes were established to whistle and bubbling. Then inhibitory compound was introduced. Consisting of a sight and noise of a rotating disc, further denoted as rotor, acting for 5 seconds. Conditioned inhibition was established after 40 applica-

tions of this compound. After 90 applications of this compound the experimental procedure was altered in such a way that only bubbling was applied as a positive stimulus and whistle alone was not used; it was applied only in combination with rotor and without reinforcement. The series of these experiments lasted for 27 days, the inhibitory compound being applied 4-5 times in each session. Throughout this series it was applied 111 times. The inhibitory reflex to the compound was never disinhibited.

In the crucial experiment following this series the compound rotor — whistle was applied 5 times in succession, and immediately afterwards whistle alone was tested. As seen from the record of this experiment (Fig. 2), in response to whistle the dog immediately raised his leg and
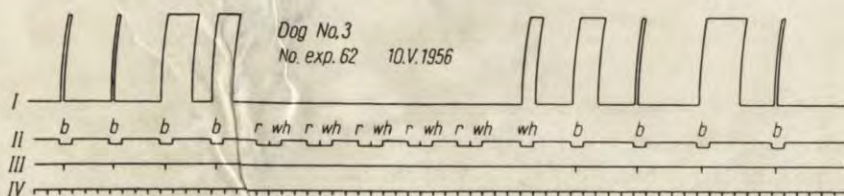
Fig. 2. The protocol of the experiment in which stimulus S_1 (whistle) was presented after repeated applications of the inhibitory compound S_0S_1 in the series of experiments.

I — lifting the foreleg and placing it on the foodtray, II — conditioned stimuli: b — bubbling: wh — whistle (S_1); r — rotor (conditioned inhibitor S_0), III — food reinforcement, IV — time in 5 sec. Note that whistle being applied after many repetitions of the compound rotor-whistle and four applications of this compound in the present experiment produces normal positive reaction.

placed it on the foodtray, and, as food was not given, he scratched at the foodtray and stared at the bowl. In other words the dog displayed a full alimentary reaction to whistle without any trace of inhibition.

Dog No. 4. The experiments with this dog took exactly the same course as experiments in dog No. 3, except that in the inhibitory compound between the conditioned inhibitor and the conditioned stimulus an interval of 5 seconds was introduced. In consequence the "individual" character of the conditioned stimulus in the compound was even better preserved than in the previous experiments. Nevertheless, the results were unambiguous: the repetitive application of the inhibitory compound, without application of the corresponding conditioned stimulus alone, did not produce extinction of the excitatory reflex to this stimulus.

When this series of experiments had been completed, a new series was carried out in which no positive conditioned stimuli were applied

at all, and in 11 experimental sessions only the inhibitory compound was given several times a day (altogether 42 times). On the 12th day, after 4 applications of this compound, the conditioned stimulus alone was given. In spite of the inhibitory background against which it was
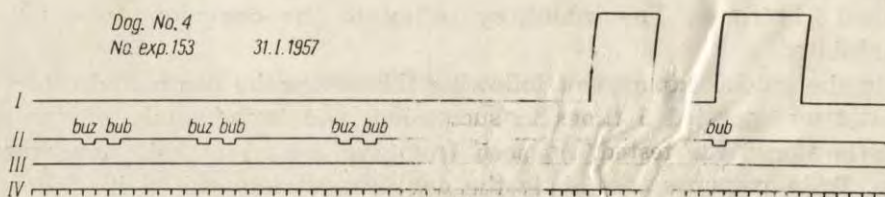
Fig. 3. Application of conditio. ... is S_1 afte... ... of the compound S_0S_1 pre... ... a series ...

applied, the stimulus elicited a full-sized ... ...ction (Fig. 3). So, even the drastic handicaps to which the ... conditioned reflex to this stimulus was subjected did not exert a ...fluence on its effect.

In five dogs Nos. 3, 4, 5, 6 and 7. ... the elaboration of the inhibitory reflex to the compound S_0S ... ...nce to extinction of the conditioned reflex to stimul- ... that to a control conditioned stimulus S_2, was inves... ...Nos. 3 and 4 extinction was carried out immediately after the ... ...xperiments described in the previous section, i.e. repeated app... ... of the inhibitory compound S_0S_1, and no application of s... ...parately. In other dogs extinction was conducted simply ... ...ory reflex to S_0S_1 had firmly been established.

The results of these experiments are pre... ...ted in Table I. As seen from this table the numbers of trials required to the extinction of the conditioned reflex to stimulus S_1 and S_2 are more or less the same. The slight differences in the course of extinction were due to the differences of relative strength of the stimuli and were independent of whether or not they belonged to the inhibitory compound. Since bubbling of water was a somewhat weaker stimulus than the metronome, its resistance to extinction was lesser.

IV

In two dogs, Nos. 8 and 9 the experimental procedure was somewhat different. First instrumental conditioned reflexes to metronome and bubbling were firmly established then we discontinued to apply bubbling alone and instead of it we introduced the compound composed of buzzer (5 sec.) and bubbling (5 sec.) applied without reinforcement. In other words, no differentiation of the conditioned stimulus from the inhibitory compound as it had been the case in the previous series was established, but instead a sort of extinction of the conditioned stimulus was carried out.

At the beg: the compound eli ited a positive conditioned reaction which . ppeared af er 13 trials in one dog and after 22 in the other.

After 85 applications of the compound buzzer-bubbling during 53 experimental sess. was again applied separately. It elicited the positive reaction a prolonged latent period. The reaction was extinguished after pplications of the stimulus without reinforcement in No 8 and three in dog No. 9. On the other hand, chronic extinction of the metronome was achieved after only 12 trials in dog No. 8 and after 8 trials in dog No. 9 (Table I).

Table I

Resistance to extinction of conditioned reflex to stimulus (S_1) participating in the inhibitory compound ($S_0 S_1$) as compared to a control conditioned stimulus (S_2)

No. of dog	S_0	S_1	S_2	Trials to extinction			
				to S_1		to S_2	
				1st neg. response	full extinct.	1st neg. response	full extinct.
3	rotor	whistle	bubbling	25	25	23	26
4	buzzer	bubbling	metronome	4	4	5	5
5	buzzer	bubbling	metronome	5	5	8	8
6	buzzer	metronome	bubbling	6	6	6	6
7	buzzer	metronome	bubbling	7	11	5	9
Average				9.4	10.2	9.4	10.8
8	buzzer	bubbling	metronome	3	3	9	9
9	buzzer	bubbling	metronome	4	4	13	13
Average				3.5	3.5	11	11

These experiments show that when, after the formation of the positive conditioned reflex to stimulus S_1, we apply this stimulus as a part of the inhibitory compound S_0S_1 only, and the stimulus S_1 alone is no more applied, then this stimulus unequivocally acquires inhibitory properties.

DISCUSSION

The basic result of this paper is that when a compound composed of conditioned inhibitor S_0 and conditioned stimulus S_1 is differentiated from conditioned stimulus S_1 applied separately, then the compound S_0S_1 and stimulus S_1 become, so to speak, quite independent one from another. This may be proved by the fact that repeated application of the compound does not affect the positive response to stimulus S_1, even if this stimulus is not applied during the whole series of such experiments. Under these conditions stimulus S_1 does preserve its full conditioned effect and additionally its resistance to extinction is as strong as this of control stimuli. In other words stimulus S_1 applied in compound with S_0, and applied separately behave as quite different stimuli producing different responses. If the two components of the compound were applied simultaneously, one could admit that stimulus S_1 looses its individual character when presented together with stimulus S_0. But since stimulus S_1 was always applied a f t e r stimulus S_0, and in some experiments even with 5 seconds interval, this possibility is ruled out. On the other hand, if in the first training inhibitory compound S_0S_1 is not differentiated from stimulus S_1 applied alone, then the inhibitory character of this compound is transferred to the stimulus S_1 when this stimulus is applied separately. In such a case resistance to extinction of the stimulus S_1 is significantly reduced.

The results of our experiments seem to indicate that after the differentiation between the compound S_0S_1 and stimulus S_1 has been established, these two stimuli form different entities independent one from another and possessing separate cortical "representations". Consequently the inhibitory properties of the compound S_0S_1 cannot be considered as a result of a balance between the properties of stimuli S_0 and S_1 applied separately as it had previously been supposed by K o n o r s k i.

SUMMARY

1. This paper is concerned with the interrelations between the inhibitory compound composed of conditioned inhibitor (S_0) and conditioned stimulus (S_1) and the conditioned stimulus (S_1) applied separately.

2. Repeated application of the inhibitory compound S_0S_1 does not produce the extinction of the positive conditioned reflex to stimulus S_1.

3. Resistance to extinction of stimulus S_1 is the same as to a control conditioned stimulus not participating in the inhibitory compound.

4. If the inhibitory conditioned reflex is formed to the compound S_0S_1 without differentiating it from stimulus S_1 applied separately, the resistance to extinction of the stimulus S_1 is considerably reduced.

5. The theoretical implications of these results are discussed.

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"AUGMENTED SECRETION"
IN UNCONDITIONED SALIVARY REFLEXES IN DOG

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The term "augmented salivary secretion" was introduced by Langley (1889) to denote Bradford's (1888) discovery of increased salivary secretion produced by sympathetic stimulation after previous stimulation of chorda tympani or of the Jacobson's nerve. This term was later extended by Babkin (1950) and "applied to the increased effect of any two successive stimulations of the same or of different secretory nerves of the salivary glands" (Babkin 1950, p. 768.)

The aim of our study was to find this phenomenon in chronic experiments on dogs, using gustatory stimulation by weak acid solution. In other words, we wanted to determine the role of the "augmented secretion" in the reflex activity of the parotid gland. This is of great importance for the method of salivary conditioned reflexes for the following reasons. Conditioned salivary reflexes vary in the course of the experimental session in their size and latency. We have already shown that some variations are artifacts caused by the retention or rejection of saliva from salivary duct (Sołtysik 1957, Sołtysik and Zbrożyna 1957). It seemed possible, and some preliminary experiments of Bruner and Jankowska (pers. comm.) and Bruner and Kozak (1954) suggested it, that some variations of salivary reflexes are due to unequal intertrial intervals. Namely, the shorter the interval the greater the facilitatory influence of the preceding stimulation and the greater the salivary reflex elicited by actual stimulation. Using the equal intertrial intervals is not a remedy here, because there are usually both positive and inhibitory trials in

conditioned reflex experiments and again the time lapse between the positive stimuli varies depending on interposed inhibitory trials. Thus, without accurate knowledge of the effects of preceding on successive stimulations in salivary reflexes, it is impossible to evaluate properly the actual size of those reflexes.

MATERIAL AND METHODS

Two adult mongrel male dogs, Wilczek and Łysy, were used. In both animals "shortened" salivary duct fistulae of parotid gl... .s were prepared by our method (S o ł t y s i k and Z b r o ż y n a 1957). B...d.s ... . hole was operatively made 0.5 cm. in diameter on the ch..k ... ...la; through this hole an acid solution was introduce 1 au ... ...e tube) into the mouth as an unconditioned ag.. .. ..g, Wilczek, we performed also a carotid artery loop ... ...'s method (1911) to enable the recording of pulse .. .. in a soundproof conditioned reflex chamber. D... ... ... were accustomed to the experimental situa.. ... ...lating devices.

Salivation w.s r... ... ...d (K o z a k 1949, 1950). Pulse rate and breathing w... ... ...n a kymograph. A 0.4 per cent solution of lactic acid ... ...e each experimental session and care was taken to obtain ..e pl. = 2.6 (...e 2.45 to 2.75). The solution was introduced into the mouth ... a co..an. rat. 3 ml. per second. The stimulation
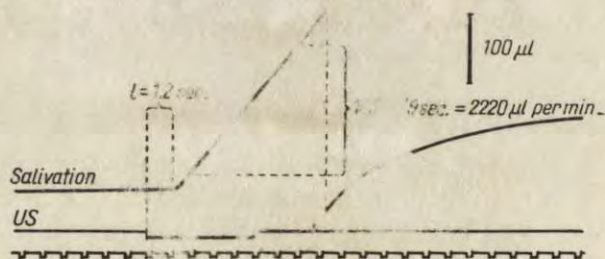
Fig. 1. Measurement of the rate an.' .atency of salivary reflex.

The voluminographic record by Kozak's sia'o.. .. is presented schematically. Slope o. the tracing curve corresponds to the rate of s.. ... . Way of measuring latency and rat. of salivary reflex is shown.

lasted 5 seconds, i.e., 15 ml. of solution was introduced in each trial. Each daily session consisted of 8—16 trials. The following parameters of response were measured:

1) rate of secretion during first 10 seconds of response,
2) latency of the secretory response (see Fig. 1),
3) and in one dog, amplitude of cardiac response, i.e., the rise of pulse frequency during stimulation as compared with the prestimulus level.

The minimum intertrial interval was determined by the minimum time required for complete disappearance of secretion elicited by the preceding stimulation; this

was 2 minutes in Wilczek, and some 3 minutes in Łysy. The salivary and cardiac responses after these short intervals were compared with those after intervals of 4, 8, and 16 minutes. All results were statistically analysed with the "t" test.

RESULTS

The results obtained showed that there is a close relationship between the length of intertrial interval and the secretory response. The longer the interval, the lower the rate of salivation and the longer the latency of this response (see Fig. 2 and 3, and Table 1). The rate
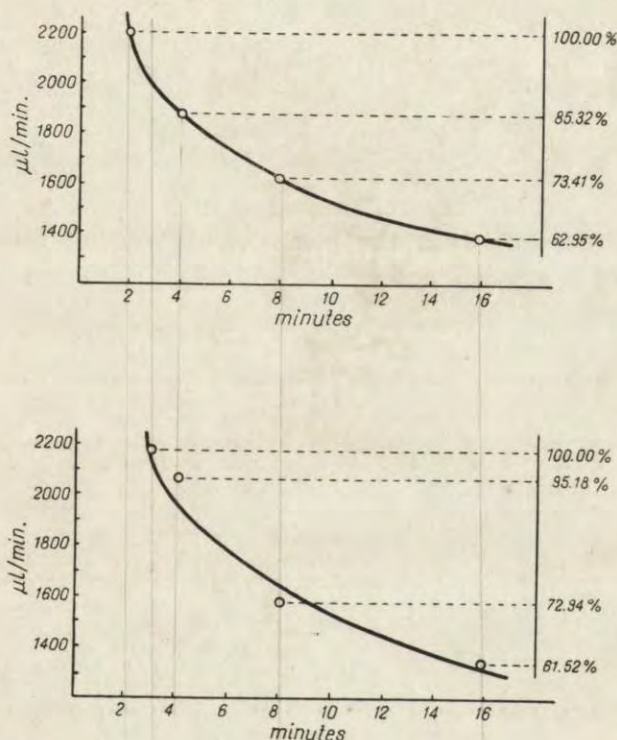
Fig. 2. "Augmented secretion" in reflex activity of parotid gland in dog.

The rate of salivation (ordinates) is plotted against the length of the preceding intertrial interval (abscissae). In both dogs quite similar curves are obtained, showing decreasing rate of salivation with increasing rest period of the gland. Upper curve from Wilczek, lower from Łysy.

of salivation plotted against the increasing time of intervals gives a regular, negatively decelerated, exponential-like curve. It approaches an asymptote amounting to about 60 per cent of the rate of salivation at the shortest interval. Further prolongation of the intertrial intervals

did not decrease the rate of salivation. All four points of each cvururve
in Fig. 2 differed significantly one from each other (except for t the
two first points in Łysy).
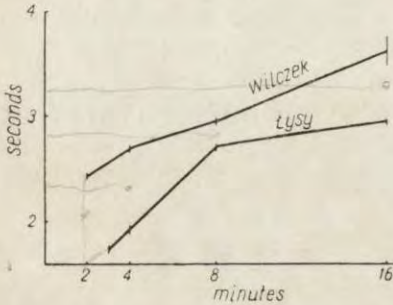
Fig. 3. Latencies of salivary urncnconditioned reflexes obtained afterr σ different rest periods.

Latencies of salivary reflexes (or (ordinates) obtained after increasing intinter-trial intervals (abscissae) are sshoshown in two dogs. There is evident lenggthgthening of latency in reflexes after ldonlonger rest periods. Vertical lines corresspcspond to ± Standard Error of a given vvalvalue.

The latencies of salivary reflexes increased approximately linearararly,
and the differences between the mean values for all intervals (wiwith
the exception of intervals 3 and 4 minutes in Łysy) differed significamthtly.

Table I

Rate of salivation (in microliters per minute) elicited after different
rest periods

Dog	Intertrial interval (min.)	Rate of salivation	Significance of differences			
Wilczek	2	2202 ± 23				
	4	1877 ± 75				
	8	1618 ± 60				
	16	1381 ± 67				
Łysy	3	2175 ± 34				
	4	2075 ± 73				
	8	1590 ± 59				
	16	1341 ± 53				

* = p < 0.001   ** = p < 0.02   ns = p > 0.05

As far as the cardiac reflex is concerned (Fig. 4), no differences were found between reflexes after short and long intertrial intervals. There was a slight though insignificant increase of the cardiac response after

Fig. 4. Cardiac responses to introduction of acid into the mouth.

Cardiac responses, measured as difference in heart rate during and before stimulation, are not affected by the varied length of the preceding intertrial intervals. Vertical lines (at the top of each column) denote standard errors.
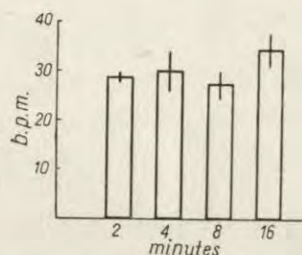
the longest interval. This was probably due to a lower pre-stimulus level or to an increased concentration of acid in the mouth — as salivation was much lower in the reflex following the longest interval.

DISCUSSION

While the phenomenon of "augmented secretion" has been known for more than 70 years in the nerve-gland preparation, the presence of it in chronic experiments on unanesthetized dog was not systematically studied. This phenomenon was previously observed in alimentary conditioned (B r u n e r and J a n k o w s k a, pers. comm.) and unconditioned reflexes in dogs (B r u n e r and K o z a k 1954a), however, without any statistical analysis of the reliability of this observation.

The use of lactic acid as an unconditioned stimulus enabled us to avoid the effect of satiation which was previously shown to influence greatly the rate of the conditioned and unconditioned salivation (S o ł-t y s i k and C z a r n e c k a 1960). The precise method of both recording and stimulation gave us a clear result which closely corresponds to observations in acute experiments (B r u n e r and K o z a k 1954b, 1954c).

All these facts show that the long lasting traces of stimulation described in nerve-gland preparation also exist in the normal animal and influence the actual size of secretory reactions.

The absence of any central factor in this phenomenon is suggested by the fact that the cardiac reflex to the same stimulus (introduction of acid into the mouth) is quite insensitive to variation of length of the intertrial interval. This may be explained by differences in the physiology of the two organs. The salivary gland in the dog is activated by

intermittent stimuli and may stop its secretory activity when no such stimuli are present. Therefore the functional state and readiness to respond vary in this gland from the state of maximal secretion to that of full rest. The heart, on the other hand, works spontaneously and the vagal nerve, which is chiefly responsible for cardiac acceleration in reflexes to different external stimuli (W i g g e r s 1949, B o n d 1943, D y k-m a n and G a n t t 1959), maintains a steady inhibitory influence, i. e., both the effector and its peripheral innervation work continuously. Besides this, the cardioacceleration is not effected by the incoming impulses but merely by the release from the tonic inhibition. In consequence, there are no conditions for "warming-up" effects in the peripheral link of cardiac reflexes.

All this confirms the interpretation that the changes observed in salivary reflexes are in fact peripheral glandular effects depending on the traces of the activation in glandular tissue.

However, this fact was scarcely taken into account in previous conditioned reflex experiments. For instance, the so called inhibitory aftereffect, consisting in the positive conditioned stimulus eliciting a smaller effect when presented after the inhibitory stimulus, was thought to be due to some central processes. However, one might hypothesize that this diminished salivation could be caused, at least partially, by the prolongation of resting period of the gland. Similarly, the "augmented secretion" phenomena may contaminate the unilateral salivary reflexes in the A b u l a d z e's method of isolated tongue (1953). Therefore we think, that future experiments on salivary reflexes might be better controlled in this respect.

SUMMARY

Effects of varied lengths of intertrial intervals on salivary and cardiac unconditioned reflexes were studied. It was shown that the phenomenon of "augmented secretion" is present in normal unanesthetized animals and influences greatly both the rate and latency of salivary reflexes. The cardiac reflexes in contrast, are not characterized by any sign of a "warming-up" effect and do not depend on the length of the intertrial interval ranging from 2 to 16 minutes. The importance of these facts for the proper evaluation of the results obtained in conditioned salivary reflex experiments is discussed.

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RETURN REACTION VERSUS ONE TRIAL LEARNING

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In a previous paper of this series it was established that a rat which ran a certain way in one direction was able to choose this way, if it had to return back to the starting place. We have called this sort of behaviour "return reation". When the route was changed from day to day the correct return reaction was to a certain degree affected by the memory of the return reaction from the preceding day (Ł u k a s z e w s k a 1961). In the present paper we have investigated the effect on the return reaction of the preceding reactions occurring in the same experimental session.

MATERIAL AND METHODS

The animals were male and female white rats. They were used in the experiments described in the previous paper (Ł u k a s z e w s k a 1961). Experimental set-up and the procedure were generally the same as those in the previous study. The same elevated mazes A, B, C, and D were applied (Fig. 1). The mazes A, B and C had two starting platforms S_1 and S_2 screened with the wooden walls E_1 and E_2. A small experimental cage was placed on one of the platforms. The cage was opened on the side adjacent to the screen which was fitted with a two-way door. The maze D had only one unscreened platform S. The cage used in this maze was opened on two opposite sides. At a certain distance from the choice-point C there were two walls E_1 and E_2. In a given experimental session the path to the food was determined by leaving open the proper doors in the cage and in the proper wall.

The rat was confronted with the same task as in the previous investigation. He had to return to the starting platform the same path he had taken going to the food. In the present study, however, the starting place was changed during each experimental session. After several starts from one starting platform, the cage with the rat was transferred to the other platform. It was done while the
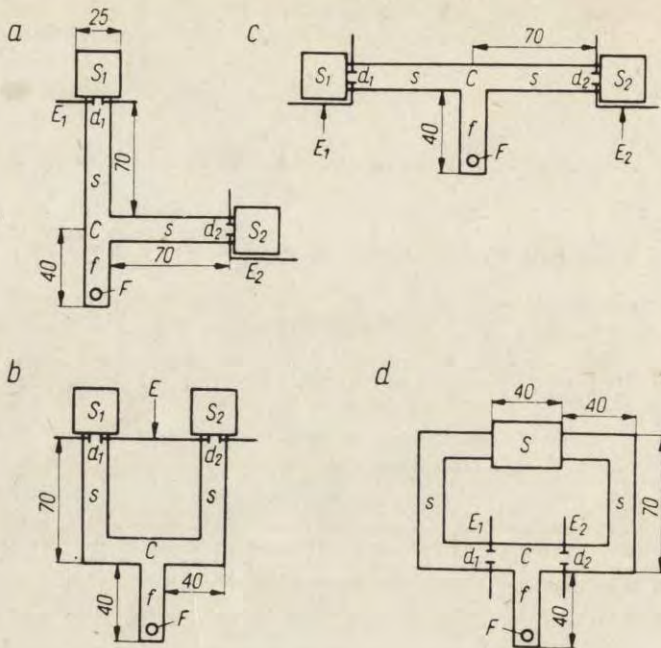
Fig. 1. The floor plan of mazes A, B, C, D.

S, S_1, S_2 — starting platforms, s — starting path, F — cup with food, f — food path, C — choice-point of return route, E, E_1, E_2 — wooden screens, d_1, d_2 — two way doors in the screen.

rat was eating. At first he displayed an orienting reaction but soon he got accustomed to this procedure. In the maze D, which had only one starting platform, the path leading to the cup was changed instead of changing the starting place. This was achieved by locking one door and opening another one both in the cage and in the screen.

Two sets of experiments were carried out. They differed from each other in the distance between the cup and the choice-point.

The first set contained 4 series of experimental sessions, each on a different group of rats and on a different maze. The number of animals on maze A, B, C, D were 6, 7, 6 and 15 respectively. 5 trials were applied daily, the starting place was changed after the second trial of each experimental session. The cup was placed at a distance of about 40 cm. from the choice-point.

The second set contained 3 series of experimental sessions performed on the same group of rats as in the series on maze D in the first set of experiments. In series I the distance between the cup and the choice-point was about 40 cm., in series II — about 25 cm., and in the series III — about 100 cm. Experiments of the first set on maze D were considered as series I. Except for the difference in the distance between the cup and the choice-point the procedure was the same as in the experiments of the first set.

In both sets each series consisted of 10-experimental sessions. The schedule of experiments changed from day to day from RRLLL to LLRRR (R — start from right platform, L — start from left platform). Thus, in the first trials of each experimental session the cage was placed on the same starting platform as in the last trial of the previous day.

The correction method was applied, i.e. the rat could correct his error.

RESULTS

The first set of experiments

Each experimental session consisted of 5 trials. The starting place was changed after the second trial. The results for all experimental series are presented in Fig. 2. The columns represent the percentage of
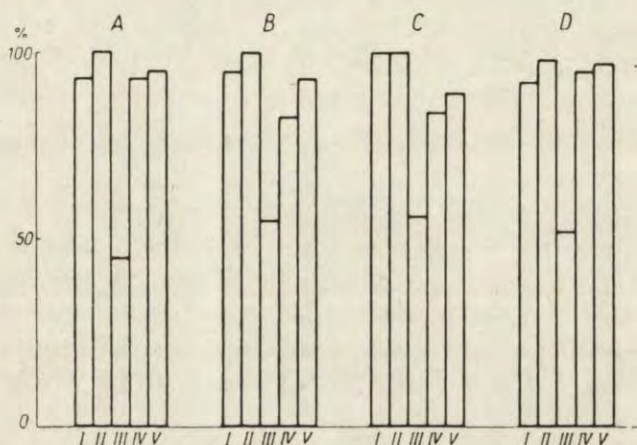
Fig. 2. The comparison of the return reactions on mazes A, B, C, D.

I, II... — successive trials. Each column represents the percentage of correct return reactions in the respective trial. After the second trial in each experimental session the starting place was changed.

correct return reactions in all the rats in all experimental sessions for a given maze. Individual columns denote successive trials. It is seen that the percentage of correct reactions is more or less the same for given trials in all the series. In the first trials the rats choose the correct route in more than 90% of cases, in the second trials their reactions are always correct. In the third return runs the rats return to the platform from which they have started only in about 50% of cases while in the remaining 50% they choose the previous route. In the fourth and fifth trials gradual improvement occurs but the level of two first trials is not attained.

If the choice of the return route was determined only by the memory of the route towards food, the rat should find his way to the cage independently of on which platform it is located. The results obtained in the third trials in which there was a change in the starting place show that there is also another factor influencing the choice of a route. It is clear that this factor is the memory of the return route ran in the previous trials. This memory is due to one trial learning. Interaction of both factors allied or antagonistic, reflects on the results of individual trials.

In the first trial of a given day the choice of the return way is chiefly determined by the memory of the way towards food. In consequence the percentage of correct responses is high. In the second trial the alliance between the memory of the preceding return reaction and the memory of the way towards food results in nearly all returns being correct. In the third trial these two factors become antagonistic: the rat remembers both the way which he ran towards food and the previous return way. Since the correct and incorrect reactions are equally frequent, one can suppose that both these factors are of an equal strength.

Since choosing the incorrect route the animal cannot immediately return to the starting place, such a return is inhibited and the correct return reaction takes the upper hand. In the fourth and fifth trials the number of correct runs gradually increases again since both factors again work in alliance. However, the memory of the return way in the first trials lowers the number of correct returns which do not achieved 100%.

The struggle between the one trial learning and the correct return reaction is different in different individuals. This difference is particularly distinct in the third trials: in one of the rats all the runs in these trials were correct, while another one chose the wrong route in all experiments in this series. But sometimes the same animal succeds in the critical third trial, while he fails in a correct choice in the fourth or even fifth trial. In other words the competition between two memories, one due to one trial learning and the other due to choosing the way to food is rather complicated and lasts for several successive trials. For illustration of this relationship all sorts of reactions in the third, fourth and fifth trials of all series are presented in Table I. As seen in this table, in majority of cases (if the eight row is not taken into consideration) one or two wrong choices were followed by correct responses (row 5 and 2). At times, correct and incorrect responses appeared alternately (row 3 and 6). Very rarely all three runs after the change of

starting place were incorrect (row 1). Only in a few cases incorrect responses occured at the end of experimental session, after one or two correct choices (row 4 and 7).

Table I

Eight possible combinations of correct and wrong responses in three trials following the change of starting place

Combination / Trials	1	2	3	4	5	6	7	8
III	—	—	—	+	—	+	+	+
IV	—	—	+	—	+	—	+	+
V	—	+	—	—	+	+	—	+
Frequency	6	12	4	2	118	7	2	135

+ denotes correct return run, — denotes incorrect return run.

Since in the third trials the animals are under the influence of two conflicting factors their behaviour afterwards reveals some abnormalities. It consisted mainly in refusing to leave the cage at the end of the experiment. The number of hesitation in the choice-point was increased in the third trials.

The second set of experiments

In this set of experiments the distance between choice-point and cup was changed. Experiments of the first set on maze D were considered as series I; the distance between choice-point and cup was here 40 cm. In series II this distance was 25 cm, i.e. nearly the length of the rat's body. In series III the distance was 100 cm. All these series were carried out on the same animals and the procedure was the same as in the experiments of set 1.

The results of these experiments are presented in Fig. 3. As it is seen, the number of correct return runs in the first and second trials is the same in all these series. On the contrary, the difference between these series is very pronounced in the third trials. After the shortening of food path the rats improved considerably *. On the other hand elonga-

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* It should be, however, noticed that according to our later experiments (Ł u-k a s z e w s k a, in preparation) the animals are able to overcome their perseverative errors in the course of experiments. Therefore the increase of correct responses in the series II may by partially due to this sort of training.

tion of food path caused as many as 80% errors. These differences were attenuated in the fourth trials and disappeared in the fifth one.

The longer the food path the stronger the neurotic behaviour in the animals. While in series I only in two cases the animals did refuse to

Fig. 3. The influence of the distance between the cup and the choice-point upon the return reaction.

Dashed, white and black columns represent the first, the second and the third series of experiments respectively. In series I the food path was about 40 cm., in series II — 25 cm. and in series III — 100 cm. a — trials before the change of starting place, b — trials after the change of starting place.

leave the cage after the third trials, in series II only in one case, in series III there was not less than eight such refusals.

DISCUSSION

In the choice of the return route the rat may utilize cues which he noticed either while going for food or in the return reaction of the preceding trial. Both these reactions are based on recent memory. The return reaction is based on memory of the way he went for food. On the other hand, he remembers the preceding return reaction on the basis of one trial learning in each experimental session.

Whether the rat is guided in his return way by the first or second kind of memory traces depends on the experimental situation. In the first paper of this series (Lukaszewska 1959), in which a perpendicular maze had been used, the rats were guided only by memory of the preceding return way perhaps due to their inability to choose the

passed way in the perpendicular plane. In experiments with horizontal maze it was proved that the rats have no difficulty in choosing the passed way while the memory of the return route of the previous day only slightly disturbs this reaction (Łukaszewska 1961).

In the present paper the interference of return based on one trial learning on the correct return reaction was investigated in more detail. It was found that after change of starting place both these factors are in operation, and it is amazing how much the one trial learning can disturb the correct choice.

Ławicka (1959) has found when investigating in dogs and cats the delayed reactions by the method of triple choice that the most common errors made by these animals are so called perseverative errors: in some trials the animals after being released at the end of the delay period went not to the signalled foodtray but to the one reinforced in the last trial. Cats were even worse in this respect than dogs. The number of these errors increased considerably after prefrontal ablations (Ławicka and Konorski 1961). The perseverative tendency was also observed in monkeys with frontal lesions (Brush, Mishkin and Rosvold 1961).

Comparing our results with those mentioned above we may suppose that the strong tendency of rats to repeat the same return way may be connected with their lesser development of the frontal area.

The tendency to repeat the previous return way depends very much on the time lapse between two trials. An interval of 1—2 min., i.e. the interval between two successive runs is more harmful for the correct choice than an interval between two experimental sessions (24 hrs.).

Also lengthening the distance between choice-point and food cup increased significantly the tendency to perform one trial learning errors. Perhaps the balance between the two factors after the change of starting place is so labile that it may he changed even by a small complication of the task. Analogous facts were also found by Ławicka (1959).

At the outset of the experiments the question was asked whether the rat is able to find the return way to the starting place, or not. The answer is that he is able to do so in horizontal plane. However, it appeared that the rat attempting to get as quickly as possible to the place where he can eat his food, utilizes various kinds of abilities. It seems that repeating the successful return run is more primitive than the proper return reaction, and that this is the tendency which the animals most readily make use of.

However, if there is no opportunity to use this cue (e.g. in the first trial of a given session) he is quite able to choose the way he went to food.

SUMMARY

The effect of the change of starting place on the return reaction in white rats was investigated on 4 different elevated mazes.

1. In trials immediately after the change of starting place the number of correct return reactions was about 50% smaller than in trials before the change.

2. The incorrect reactions after change of starting place were caused by the memory of return route from the trials before the change (one trial learning).

3. The tendency to repeat last successful run was inhibited during each experimental session.

4. The return reaction was influenced by the distance between the food and the choice-point. The shorter the distance, the greater the number of correct return reactions.

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STUDIES ON HIGHER NERVOUS ACTIVITY IN CHICKENS.
III. THE DIFFERENCES IN CONDITIONED EXCITATORY
AND INHIBITORY ALIMENTARY REFLEXES BETWEEN CHICKENS
OF THE LEGHORN AND PERVOMAISKAIA BREEDS *

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In the recent years, an increasing number of papers has been pub-
lished on breed and other intraspecific differences in behaviour of ani-
mals. Interest in this problem is understandable because showing these
differences in behaviour, as well as success of selection for any be-
haviour trait are methods of proving that behaviour is heritable (H a l l
1951, F u l l e r 1960).

The majority of experiments on this problem was performed on
rodents, some on dogs and only a few on hens. A l t e v o g t (1951)
compared hens and cockrels of 6 breeds of different body weight, rang-
ing from 800 gm. (Bankiva) to 2,500 gm. (Brahma) and found that the
ability to discriminate between figures of different colours and shapes
was not identical in various breeds. In a simple test (discrimination of
2 figures) the required criterion of learning was reached sooner by light
hens than by heavy ones. On the simultaneous exposition of several
figures the task was mastered quicker by hens of heavy body weight.
The author concluded that the capacity of discriminating objects was
related to the absolute weight of brain in the representatives of dif-
ferent breeds.

Extensive studies on the behaviour of adult hens of different breeds

were carried out by P o n o m a r e n k o (1958a, 1958b). She found that
in contrast to the Leghorns the excitatory conditioned reflexes in hens
of Pervomaiskaia breed were markedly resistant to changes in the
experimental situation (such as: changing of alimentary excitability,
distracting stimuli and experimenting late in the evening). Also the in-
hibitory responses to differential stimuli were in the Pervomaiskaia hens
less affected by the increase of alimentary excitability. The transforma-
tion of the positive conditioned stimuli into differential ones and vice
versa was established sooner in the Pervomaiskaia hens than in the
Leghorns. The author compared these differences with other character-
istics of the investigated breeds: body weight, egg production, food in-
take, and duration of hypnosis induced by placing the birds upside down.
Only the latter index was found to vary conversely to that of the stabi-
lity of the conditioned excitatory reflexes.

Almost all our knowledge on breed and strain differences in beha-
viour were obtained on adult animals. Some authors used young animals
for experiments but only to show that given treatment in infancy has
a different influence on the adult behaviour depending on breed (K r u-
s h i n s k i i 1946, K i n g and E l e f t h e r i o n 1959).

Behavioral differences of young animals associated with breed were
described in a series of papers from Roscoe B. Jackson Memorial Labor-
atory (S c o t t and M a r s t o n 1950, F u l l e r 1953, S c o t t 1954, S c o t t
and C h a r l e s 1954, F r e e d m a n 1958). The authors bred puppies
of several breeds under similar conditions and compared their behaviour
at different stages of development. According to S c o t t (1954) 5 weeks
old puppies of the Basenji showed an obvious fear reaction to the human
voice, whereas Cocker spaniels did not. Later on, at the age of 13—15
weeks, puppies of Basenji became more agressive on the sight of a per-
son and reacted by an increased pulse rate to manipulation (weighing).
Heart rate changes induced by the appearance of a person were much
more stronger in Basenji than in Cocker spaniels at the age of one year,
whereas an increase of the heart rate after a sudden noise reached the
same level in both breeds (F u l l e r 1953). Puppies of the Basenji breed
solved the simple task of going round a barrier to get food muche easier
than spaniels (S c o t t 1954).

The differences observed between breeds increased with age as well
as during the course of training (S c o t t and C h a r l e s 1954). On the
other hand K i n g and S h e a (1959) observed remarkable differences
in the maze behaviour of two forms of deermice at the age of 10 or 14
days, whereas afterwards those differences disappeared. The authors
ascribe this to differences in rate of development of locomotion capacity
between the investigated subspecies.

MATERIAL AND METHODS

Chickens of two breeds, White Leghorn and Pervomaiskaia, were used for experiments. The Pervomaiskaia breed was produced in the USSR by crossing the indigenous Iurlovskaia Hens with Rode Island red and Wyandotte. Hens of the Pervomaiskaia breed are noted for their high body weight, stron constitution and high eeg production in winter.

In Table I several indices of the chickens studied are given.

Table I

Body weight of chickens in growth period, age of pullets
at the laying of first egg and annual egg production

Breed	Sex	Number of individuals	Body weight (gm) in the age			Age of the first egg	Annual egg production
			60 days	120 days	180 days		
Leghorn	♀♀	8	530	1 356	1 758	162.5	154.7
Leghorn	♂♂	8	660	1 653	2 092	—	—
Pervomais- kaia	♀♀	8	640	1 544	2 051	197.1	149.2
Pervomais- kaia	♂♂	8	724	1 904	2 602	—	—

Chickens were hatched on the same day and reared in one flock under similar conditions, but females were separated from males. As follows from Table I the experimental chickens were typical representatives of their breeds.

The experiments were performed by the method of conditioned alimentary motor reflexes described in previous publications (Z i e l i ń s k i 1960a, 1960b). As a measure of the conditioned reaction we took the maximal period of action of the conditioned stimulus minus the latency of conditioned response. The response was immediately reinforced with food. A more detailed description of this method of calculation of magnitude of conditioned motor reflexes was given in the first paper of this series (Z i e l i ń s k i 1960a).

In the beginning the animals were accustomed to the experimental situation i.e. orienting and defensive reactions were extinguished and the conditioned motor reflex of pecking a lever was established. In the initial experimental sessions food was in the food-bowl all the time. When the birds became accustomed to the exchange of bowls and behaved quietly, food was removed from the bowl. Usually the removal of food led to a more or less persistent search for food: scratching, pecking

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the empty bowl and the area around it. Pecking the lever was immediately reinforced by food. To facilitate the task of the animal, bits of food were left on the lever. In this situation the conditioned reflex of pecking the lever was established after a few trials. Afterwards this response appeared at once when the filled bowl was replaced by an empty one.

In the next stage of training a green and red light of the same intensity were introduced as conditioned stimuli, so that pecking the lever was reinforced by food only when it coincided with the conditioned stimulus. The conditioned stimuli were presented alternately, each four times in one experimental session at 90 secs. intervals.

After 40 applications of green light, the stimulus was no longer reinforced by food and was subjected to chronic extinction. The conditioned reactions were considered to be well established when both excitatory and inhibitory responses reached the 100 per cent criterion in two successive experimental sessions.

EXPERIMENTAL PART

Differences between chickens of Leghorn and Pervomaiskaia breeds were clearly manifested in the beginning of the experiments, when the birds were being accustomed to the experimental situation. Chickens were trained until the conditioned motor reflex of pecking the lever occured several seconds after the food has been removed. This criterion was tested in 4—5 successive experimental sessions. As follows from the data of Table II, the required criterion was reached sooner in the chickens of the Pervomaiskaia breed. The difference between the two breeds is statistically significant ($p < 0.05$).

In Tables III and IV the results of subsequent stages of experiments are summarized.

Column I shows the results of 6 experimental sessions after the regular intervals between the conditioned stimuli had been introduced, both stimuli being reinforced by food. The results of the first 6 experiments in which only the red light was reinforced by food are shown in column II. Data presented in column III are the mean values from the 20—30 experiments after the excitatory and inhibitory conditioned reflexes had been firmly established.

As follows from Table III in the first two stages of training (column I and II) higher values of the excitatory conditioned reflexes were obtained in the chickens of Pervomaiskaia breed. These differences were statistically significant.

The difference in the magnitude of the conditioned excitatory refle-

xes disappeared in further training, when the positive and inhibitory conditioned reflexes became well established (Table III col. III).

Table IV shows that marked differences in the number of intertrial responses in both breeds were observed in the initial stages of training. A higher number of intertrial responses was observed in the Pervomaiskaia chickens as compared with such responses in Leghorns, and this difference disappeared after the conditioned reflexes had been firmly established.

It should be stressed that the number of experimental sessions needed for reaching the 100 per cent level of conditioned reflexes proved to be equal in both breeds (Table V).

Since a considerable individual variability was observed in this respect (number of experimental sessions necessary for establish of both positive and inhibitory reflexes was: minimum 7, maximum 34) the small differences observed between both breeds are not statistically significant.

Table II

Time (in min.) needed for accustoming the birds to the experimental situation and establishment of the conditioned motor reflex of pecking the lever

Age of chickens	Sex	Leghorn	Pervomai-skaia
Series I (2—4 months)	Pullets	88	73
	Cockerels	95	66
Series II (4—6 months)	Pullets	64	66
	Cockerels	74	50

Analysis of variance

Source of variation	DF	MS	F	P
Age (A): younger vs. older	1	2095.65	4.88	<0.05
Breed (B): Leghorn vs. Pervom.	1	2260.65	5.27	<0.05
Sex (S): pullets vs. cockerels	1	25.65	<1	Not signif.
Interactions				
Age vs. breed (AB)	1	294.59	<1	Not signif.
Age vs. sex (AS)	1	7.59	<1	Not signif.
Breed vs. sex (BS)	1	890.69	2.08	Not signif.
Age vs. breed vs. sex (ABS)	1	49.52	<1	Not signif.
Error	24	429.25	—	—

Table III

Magnitude of conditioned excitatory reflexes at different stages of training

Groups of chickens	I		II		III	
	When both conditioned stimuli were positive		In the beginning of differentiation		After establishment of excitatory and inhibitory reflexes	
	Leghorn	Pervom.	Leghorn	Pervom.	Leghorn	Pervom.
Series I ♀	16.7	13.9	16.7	21.1	24.4	23.0
Series I ♂	11.8	23.3	14.5	21.2	22.5	23.6
Series II ♀	22.0	22.4	23.5	24.6	24.1	24.9
Series II ♂	18.7	20.0	16.4	22.8	25.4	24.2

Analysis of variance

Source of variation*	F	P	F	P	F	P
A	12.04	<0.01	5.44	<0.05	10.58	<0.01
B	4.47	<0.05	10.48	<0.01	<1	Not signif.
S	<1	Not signif.	2.82	Not signif.	<1	Not signif.
AB	1.96	Not signif.	<1	Not signif.	<1	Not signif.
AS	4.66	<0.05	1.25	Not signif.	1.11	Not signif.
BS	9.17	<0.01	1.62	Not signif.	<1	Not signif.
ABS	3.88	Not signif.	<1	Not signif.	7.97	<0.01

* Lettering as in Table II.

Since the magnitude of the positive conditioned reflexes at the start of the differentation was lower in Leghorns (Table III, col. II), but at the same time there were no differences in the magnitude of these reflexes after they had been established (Table III, col. III), and the criterion of 100 per cent level of performance was reached after the same number of daily sessions (Table V) — it is obvious that the establishment of responses took place at higher rate in the Leghorns.

Likewise the extinction of intertrial responses was quicker in the Pervomaiskaia chickens (Table IV, col. II and III, Table V), than in Leghorns. Thus, the differences between the breeds, while being distinct initially, disappeared in the course of training.

After the conditioned excitatory and inhibitory reflexes had been established, the effect of prolongation (from 10 do 90 secs.) of the differential stimulus and the effects of changes in the alimentary excitability were tested. In the case of prolongation of the differential stimulus as well as of decrease of alimentary excitability no differences

between breeds were found. In the experiments in which the alimentary excitability was increased, the magnitude of the positive conditioned response was higher (p $<$0.05) in the Leghons (Table VI); however no differences were found in either inhibitory or intertrial responses.

Table IV

Number of intertrial responses at different stages of training

Groups of chickens	I When both conditioned stimuli were positive		II In the beginning of differentiation		III After establishment of excitatory and inhibitory reflexes	
	Leg-horn	Pervom.	Leg-horn	Pervom.	Leg-horn	Pervom.
Series I ♀	46.5	47.7	31.5	45.5	17.0	21.1
Series I ♂	40.3	68.0	24.7	37.8	7.4	14.1
Series II ♀	69.7	80.9	56.8	48.1	20.7	17.7
Series II ♂	49.5	69.4	27.6	49.2	7.6	12.3
Analysis of variance						
Source of variation*	F	P	F	P	F	P
A	9.69	$<$0.01	4.99	$<$0.05	$<$1	Not signif.
B	7.72	$<$0.05	4.43	$<$0.05	$<$1	Not signif.
S	$<$1	Not signif.	5.05	$<$0.05	5.47	$<$0.05
AB	$<$1	Not signif.	$<$1	Not signif.	$<$1	Not signif
AS	4.51	$<$0.05	1.07	Not signif.	$<$1	Not signif.
BS	2.67	Not signif.	2.21	Not signif.	$<$1	Not signif.
ABS	$<$1	Not signif.	4.24	Not signif.	$<$1	Not signif.

* Lettering as in Table II

Table V

Number of experiments needed for reaching 100 per cent level conditioned reflexes

Age of chickens	Sex	Leg-horn	Pervomaiskaia
Series I (2—4 months)	Pullets	19.5	18.8
	Cockerels	22.8	18.0
Series II (4—6 months)	Pullets	19.5	19.3
	Cockerels	19.7	18.8

Table VI

Magnitude of conditioned excitatory reflexes in conditions of increased alimentary excitability

Age of chickens	Sex	Leg-horn	Pervomaiskaia
Series I (2—4 months)	Pullets	26.6	26.3
	Cockerels	26.9	25.6
Series II (4—6 months)	Pullets	27.1	26.3
	Cockerels	26.7	24.8

Analysis of variance				
Source of variation	DF	MS	F	P
Age: younger vs. older	1	0.33	<1	Not signif.
Breed: Leghorn vs. Pervom.	1	8.87	7.36	<0.05
Sex: pullets vs. cockerels	1	2.70	2.24	Not signif.
All interactions	4	3.90	<1	Not signif.
Error	24	1.21	—	—

DISCUSSION

R i c h t e r (1954) compared a number of morphological and physiological properties of Norwegian rats and of Albino rats belonging to the same species and noticed that the changes in alimentary excitability exert a smaller influence upon the behaviour of the Albino rats characterized by a lower metabolism than upon the wild Norwegian rats.

In chickens of the same broods that served for the experiments described above, differences in intensity of gaseous metabolism were observed between the investigated breeds from the 4th month of life. In the earlier stages these differences were not statistically significant. Leghorns consumed more oxygen than the chickens of Pervomaiskaia breed (Z i e l i ń s k i 1960c).

Experiments with changed alimentary excitability presented in this paper, were carried out in the final stage of the experimental cycle, when the chickens were at the age of 4 (series I) or 6 (series II) months. As a result of a more intense metabolism a 24-hour starvation period proved to affect Leghorns more and caused in increase of conditioned alimentary reflexes.

The differences in the magnitude of the conditioned reflexes as well as in number of intertrial response observed in the initial stages of experiments, cannot be accounted for differences only which might result from the higher intensity of metabolism and consequently from a higher alimentary excitability in Leghorns.

As a result of procedure used to elaboration of the conditioned motor reflex of pecking the lever there was a large number of intertrial responses after the conditioned stimuli were introduced. A higher number of intertrial responses in the chickens of Pervomaiskaia breed suggests that the reaction of pecking the lever was better established in those chickens that in the Leghorns. The period needed for accustoming chickens to the experimental situation was shorter in the Pervomaiskaia breed which indicated a more rapid extinction of the orientation and defensive reactions against the experimental situation, and also a quicker development of the conditioned reflex.

In the period of accustoming chickens to the experimental situation two kind of difficulties were encountered. The slowest and most difficult was the course of training of those chickens, which showed the strongest defensive reaction to the experimental situation, that is tried to get out from the camera and run away in panic when the bowl was changed. Those chickens which were afraid of the change of bowl had serious difficulties in the elaboration and stabilization of the conditioned motor reflex of pecking the lever. The period of accustoming to the experimental situation was also long in those chickens which were indifferent to food and fell asleep as soon as food was removed from the bowl.

A strong defensive reaction and an excessive activity in the camera occured among the Leghorns and some cockerels of the Pervomaiskaia breed. A low alimentary excitability and inclination to sleep in the camera was observed in 5 pullets of the Pervomaiskaia breed and in one of the Leghorns. In general chickens of the Pervomaiskaia breed were much quieter in the camera than the Leghorns. This fact explains the shorter period of accustoming the chickens of Pervomaiskaia breed to the experimental situation and the higher stability of their reaction of pecking the lever.

In those chickens in which the defensive reaction to experimental situation was resistant to extinction, the disturbances in behaviour appeared on each change of the experimental procedure. One of those was the introduction of visual conditioned stimuli. Although the reaction of pecking the lever was well established in all chickens, some of them ceased to respond to the lever. It should be stressed that a low magnitude of conditioned excitatory reflex was observed in those

chickens which had a long period of accustoming to the experimental situation.

Thus, in our experiments Leghorns characterized by a high oxygen intake were not only much more affected by starvation than Pervomaiskaia chickens, but they were worse during the initial stages of training because of excessive activity and excitability.

R u n d q u i s t and B e l l i s (1933) found that basal metabolic rates are higher in a group of active rats than in inactive ones but they suggest that other factors besides basal metabolism are involved in level of activity. In dogs there is a clear correlation between activity and food-intake (J a m e s and M c C a y 1950). Extremely active dogs require more time to become acquainted with the experimental situation and the differences between dogs of active and inactive breeds remain during the training of both conditioned salivary responses and conditioned avoidance responses (J a m e s 1953).

Taking in account the results obtained on rats and dogs it is possible to explain all differences observed in chickens in our experiments by the interaction of activity, alimentary excitability and strength of defensive responses to the experimental situation.

We would like to draw attention to the fact, that Leghorn cockerels became accustomed to the experimental situation slower and showed a lower magnitude of conditioned excitatory reflex than pullets, whereas in Pervomaiskaia breed the cockerels mastered the experimental situation quicker. The lower indices in the Leghorn cockerels and Pervomaiskaia pullets seems to indicate that breed differences are strengthened by sex characters: the most restless were Leghorn cockerels, and the low alimentary excitability and falling asleep in camera was observed exclusively in the pullets, chiefly of Pervomaiskaia breed.

Let us compare our results with the reports of P o n o m a r e n k o (1958b). She found distinct differences between hens of Leghorn and Pervomaiskaia breeds after stabilization of conditioned reflexes. In her publications no data concerning the initial stages of experiments are reported. The changes in the experimental conditions applied by Ponomarenko were much more drastic than in our experiments. Her experiments were performed on adult hens. But, as follows from our previous publications (Z i e l i ń s k i 1959, 1960a), age is an important factor influencing the stability of the conditioned excitatory motor reflexes.

In P o n o m a r e n k o's experiments the magnitude of the conditioned reflexes after their stabilization in normal experimental conditions amounted in Leghorns to 23.3 ± 0.6 and in Pervomaiskaia hens to 25.3 ± 1.3. Slightly lower magnitudes of the conditioned excitatory

reflexes in the Leghorns than in the Pervomaiskaia hens in experiments of P o n o m a r e n k o remind us of differences observed in our experiments when the positive and inhibitory reflexes did not reach the 100 per cent criterion. When the criterion was reached the magnitudes of the conditioned excitatory reflexes in our experiments in chickens of Leghorn amounted to 23.98 ± 0.40 and of Pervomaiskaia — to 23.91 ± 0.26. This suggests that the principal reason of discrepancy is the different degree of stabilization of the conditioned reflexes in P o n o m a r e n k o's experiments and ours.

SUMMARY

The aim of this paper is to test whether the breed of chickens has any influence on excitatory and inhibitory alimentary reflexes. For this purpose experiments were performed on 16 chickens of Leghorn and 16 of Pervomaiskaia breed. Following indices were tested: time needed for accustoming the birds to the experimental situation, magnitude of excitatory and inhibitory reflexes and number of intertrial responses at different stages of training.

The following results were obtained.

1. The time necessary for accustoming to the experimental situation and elaboration the motor reflex of pecking the lever was shorter in chickens of Pervomaiskaia breed than in Leghorns.

2. In the initial stages of experiments the magnitude of conditioned excitatory reflexes were higher and the numbers of intertrial responses — smaller in the Leghorns than in chickens of Pervomaiskaia breed. After stabilization of the positive and inhibitory conditioned reflexes the differences between breeds disappeared.

3. Under conditions of the increased alimentary excitability Leghorns showed higher magnitudes of conditioned excitatory reflexes than Pervomaiskaia chickens.

The results described in 1 to 3 as well as observation of behaviour of chickens in the camera suggest that the breed differences may be explained by interaction between activity, alimentary excitability and strength of defensive reactions in chickens of the investigated breeds.

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APHAGIA AND ADIPSIA IN A DOG
WITH BILATERAL COMPLETE LESION OF THE AMYGDALOID COMPLEX

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In an earlier investigation (Brutkowski, Fonberg and Mempel, 1960) it has been demonstrated that dogs with bilateral lesions of the lateral and ventral portions of the amygdaloid complex display a marked impairment on inhibitory (unreinforced) trials in the situation in which the positive CS is reinforced with food. The assumption was made in that report that this postoperative impairment might be produced by hyperphagia described in amygdalectomized animals (Fuller, Rosvold and Pribram 1957; Green, Clemente and de Groot 1958; Morgane and Kosman 1957, 1959, 1960). In the same paper aphagia in one dog with a complete removal of the amygdala was reported.

This communication provides a detailed description of this dog. The literature contains no evidence that damage to the amygdaloid complex and adjacent structures results in abolition of food intake. We therefore consider it is worth reporting the results, even though they refer to one animal. Further exploration of the effects of amygdala lesions on food intake in some more dogs is in progress.

MATERIAL AND METHODS

Observation and training. D-8, a male spaniel weighing 15 kgms. was trained to perform excitatory (positive) and inhibitory (negative) food CRs in a sound-proof conditioned-reflex chamber. He had a parotid gland fistula and, in addition to the instrumental (type II) response, the salivary response was

recorded and measured. CR type II consisted in active placing the right hind leg on a small board. This movement was reinforced with food after a 10-second delay. In the inhibitory trials a different CS was presented also for 10 seconds but no food was given. All CSi were presented in succession (B r u t k o w s k i, F o n-b e r g and M e m p e l 1960).

Preoperatively, the dog belonged to the "unbalanced type of the nervous system" in Pavlovian terminology, i.e. his excitatory responses dominated over inhibitory responses. Although outside the conditioned-reflex chamber the dog behaved adequately, he became highly irritated when placed in the experimental situation He struggled vigorously, whined and barked, and attempted to escape. Such behaviour was particularly evident in inhibitory trials. The dog responded also between trials. He often developed neurotic disorders in which he became even more irritable. Neither differentiation nor conditioned inhibition were permanently mastered by him. He also failed in alternation (B r u t k o w s k i 1959). The training of classical defensive (type I) CRs was described elsewhere (F o n b e r g, B r u t k o w s k i and M e m p e l 1962).

From the previous observations on various species, including dog, it appears that removal of amygdala results in hypomotility, tameness and placidity (K l ü v e r and B u c y 1937; R o s v o l d, M i r s k y and P r i b r a m 1954; F u l l e r, R o s-v o l d and P r i b r a m 1957; S c h r e i n e r and K l i n g 1956). In view of this evidence we expected that removal of the amygdaloid complex in D-8 would produce a reduction of excitement and irritability and thereby enable the dog to solve the differentiation and conditioned inhibition tasks.

O p e r a t i o n s. The operative procedures were done under intraperitoneal Nembutal anesthesia with sterile precautions. The amygdaloid complex was removed in two stages, first on the right and then on the left side, separated by an interval of 6 months. The resection was performed in a manner similar to that described by F u l l e r et al. (1957).

Postoperative testing was started a week after each operation.

V e r i f i c a t i o n o f l e s i o n s. After the observation of the animal had been completed, a year following the second operation the dog was sacrificed. The brain was immediately removed and placed in formalin. Brain slices were embedded in paraffin and cut at 20 µ for staining with Nissl and Klüver techniques. From these sections the extent of lesion was reconstructed.

RESULTS

H i s t o l o g i c a l f i n d i n g s: R i g h t h e m i s p h e r e. The amygdaloid complex was removed completely. The pyriform cortex covering it ventrally was damaged as well. In addition, the lesion encroached slightly on the adjacent neocortex, the antero-ventral tip of the Ammon's horn, and the posterior part of the substantia innominata.

L e f t h e m i s p h e r e. The resection of the amygdaloid complex was also complete but, on the whole, in spite of the greatest care it was impossible to avoid additional unintended damage. Thus, the lesion on this side was more extensive than on the right and involved the posterior part of the olfactory tubercle, the antero-ventral putamen,

the antero-ventral tip of the Ammon's horn and almost the entire globus pallidus and the substantia innominata. Damage was also done to the whole length of the pyriform cortex along the ventral surface of the amygdaloid complex with a slight encroachment on the neocortex. Furthermore, the internal capsule was invaded at several points.

Cells of the dorso-medial nucleus of the left thalamus underwent a massive degeneration, and adjacent portion of the nucleus paracentralis and the ventral region of the nucleus ventralis showed similar degenerative changes. There was also a slight degeneration in the ventral portion of the medial geniculate body. A definite gliosis was seen in all these structures. The right thalamus and the caudate nucleus on both sides appeared normal. The hypothalamus was left intact on both sides; there were no changes noted in it in comparison with a standard preparation.

General examination of the brain disclosed diffuse histological abnormalities, many of which were located in distant points from the lesion. The blood vessels of the putamen, centrum semiovale, substantia innominata, the uninjuried pyriform cortex and some other regions were often swollen and surrounded with formless structures. A considerable proliferation of nuclei, as well as numerous atypical fibres at different points in the right frontal lobe indicated that degeneration had taken place there. In the ventral portion of the frontal lobe a complete demyelinization of the fibers traced from the pyriform cortex was noticeable. In the white substance of the ansa thalami above the lateral ventricle changes were found which suggested that some inflammatery process (?) had taken place there. Another spot of inflammation of approximately 1 mm. in diameter was found in the anterior composite cortex. The margin fibres of the fornix were demyelinated.

Post-operative behaviour. No changes in postoperative behaviour could be detected after the unilateral lesion on the right side. The dog continued to be irritable and disinhibited in inhibitory trials.

Following the second operation, however, two changes in behaviour were noted. First, slight impairment on motor behaviour appeared. For a few weeks a tendency to circumambulate, which presumably resulted from damage to the left internal capsule and the globus pallidus, was noted; it increased when the animal was disturbed. Thereafter it gradually subsided. Secondly, from the day of this operation onward spontaneous eating and drinking stopped. In the immediate postoperative period the animal approached food or water, smelt them and then retreated without taking them into his mouth. In most instances he even did not attempt to eat. Only occasionally he happened to be

more interested in the food he found. He touched it with the tip of his mouth but no success in eating was achieved. His emotional responsiveness towards food was remarkably reduced. He usually was not irritated with unsuccessful attempts of eating. In general he was apathetic and slow. He often passed by the food as an indifferent object although it was apparent that he was fully aware of his environment and his vision and hearing were unimpaired. A three-day starvation, repeated at different times postoperatively, did not change his behaviour. From time to time, for unknown reasons, he became excited in the presence of food. He approached it orally over and over, barked and appeared to be asking to be fed. Thus, responses towards food and fluids were not too consistent although an indifferent attitude dominated.

The animal was fed by placing food into the depth of his mouth. Most success was achieved if pieces of meat, soup or cooked cereal were pouched directly under his cheek. In some instances food was introduced with a spoon by force since the animal struggled in the feeding situation. Neither swallowing nor chewing and licking were impaired. Having food in his mouth he used his tongue and teeth. He also licked his cheeks repeatedly. The muscles of his face, too, were normal since he was able to bark and to bare his teeth if irritated. There was no motor disability of his limbs either. Thus, it was obvious that if he had attempted to pick up food, he would have done it successfully for all his motor responses which are used in the act of eating were preserved. Occasionally, he even stuck out his tongue in the manner that normal dogs do while eating but this response was unrelated to feeding. He completely ignored another dog placed nearby and did not compete with him for food. He remained submissive and apathetic even when the other dog was eating in his presence. He grimaced and growled, however, when another dog got in his way or knocked into him. Under specific circumstances "spontaneous" eating could be provoked. If while feeding the animal the spoon was removed slowly from his mouth, tongue movements happened to be elicited and small amounts of food were picked incidentally. This activity discontinued momentarily, however, and was difficult to reproduce.

Such behaviour continued anabated for five months. However, at the end of this period a sudden improvement in eating behaviour took place and c o n t i n u o u s tongue movements could be elicited. The recovery was not complete yet, and the re-appeared eating pattern was far from being normal. Special conditions were required to provoke the animal to eat. Thus, the food had to be held in the investigator's hand nearby the animal's mouth and only familiar persons could attend the feeding situation. With time further improvement took place and

the dog learned to eat from a dish placed on the floor. Nevertheless, a year after the second operation a sharp difference in eating behaviour in comparison with the preoperative state was still noticeable. Within the whole postoperative period the dog maintained his weight at a constant level.

A week after the resection of the amygdaloid complex on the second side the dog was tested in his performance on food CRs. On the first day he responded to two successive presentations of the positive CS. The instrumental response was accompanied by abundant salivation. The approach response to proffered reward was immediate: the dog inserted his mouth in the dish and attempted to eat. As he was not successful in doing it, he became irritated and tried to escape. On the following day he responded only to the first presentation of CS and subsequently he refused to react. Instead, violent struggling occurred during every food presentation. Under these circumstances continuing the experiments was impossible. Three months later salivary responses could be conditioned by reinforcement with milk introduced directly into the animal's mouth by means of a small pipe. Since the animal was very restless and excited during testing, the inhibitory (unreinforced) CS was not used.

The postoperative performance on classical-defensive CR (type I) is described separately (F o n b e r g, B r u t k o w s k i and M e m p e l 1962). Immediately after operation the defensive CR was impaired but it recovered quickly. The UCR to shock remained unchanged. The general fear reactivity was very well pronounced.

DISCUSSION

There is ample evidence that the orbito-frontal and temporal regions, including the amygdaloid complex, are concerned with feeding behaviour, gustatory functions and food and water intake. Thus M a g o u n, R a n s o n and F i s h e r (1933) produced chewing by electrical stimulation of the "most anterior regions just below the cortex of the anterior composite gyrus (orbital gyrus)", and R i o c h and B r e n n e r (1938) demonstrated salivation, irregular chewing, licking and swallowing on stimulation of the olfactory tubercle and pyriform lobe in decorticated cats. More recently, B a b k i n and v a n B u r e n (1951), K a a d a (1951), and B a l d w i n, F r o s t and W o o d (1954, 1956) confirmed these findings on cats, dogs, monkeys and human patients. P r i b r a m and B a g s h a w (1953) and B a g s h a w and P r i b r a m

(1953) pointed out that the polar-amygdaloid formations are concerned with food intake and that lesions placed in the insular cortex as well as in the anterior supratemporal plane and operculum in monkey result in ageusia. Furthermore, Bell and Lawn (1957) found that orbito-frontal lobectomy in 5 goats produced a decrease of food and water intake for about 2 months, while Green, Clemente and de Groot (1958) observed hypophagia in some amygdala cats. The postoperative impairment on eating behaviour in our dog, D-8, was even more dramatic since a bilateral complete removal of the amygdaloid complex resulted in a five-month aphagia and adipsia and the recovery was only partial. In view of this evidence and the demonstration of hyperphagia in partially amygdalectomized animals, as mentioned at the beginning of this report, one may speculate that in the frontotemporal region there are antagonistic mechanisms regulating eating behaviour.

Three conditions are to be considered with regard to the abolition of food intake in D-8:

1. Impairment of motor and autonomic responses related to food and water intake.

This impairment seems to be questionable since all the essential movements involved in eating pattern, such as chewing, licking, swallowing and smelling, remained after the second operation. Salivation was also present.

2. Decrease in appetite.

As to this point the data are not too consistent. The dog used to approach food and smelt it but, on the other hand, he often ignored it or struggled while feeding. It is likely that the approach response towards food extinguished due to the lack of reinforcement and an inhibitory response developed instead. This interpretation is supported by the fact that during conditioning sessions CRs were elicited a few times but disappeared promptly and could not be reproduced. If, however, food (milk) was introduced directly into the animal's mouth, persistent salivary CR could be established.

One may also assume that a "feeding neurosis" developed as a result of a conflict between the approach response, including such positive responses as looking at food and smelling it, and inability to eat.

3. "Eating apraxia".

It is tempting to consider the behaviour towards food in D-8 in terms of an amnestic apraxia. The behaviour consisting in approaching food but not taking it, though the primary motor responses were unimpaired,

favours this view. This impairment suggests also a lack of a "proper apprehension" of the significance of certain events, a condition which is symptomatic of apraxia. This impairment in D-8 seems to be specific and related to food intake only. Thus, "eating apraxia" may be proposed to describe such behaviour.

SUMMARY

A case of a five-month abolition of food and water intake after complete removal of the amygdaloid complex in a dog is described and discussed.

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DEFENSIVE CONDITIONED REFLEXES AND NEUROTIC MOTOR REACTIONS FOLLOWING AMYGDALECTOMY IN DOGS

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Lesions in the amygdaloid complex have been observed to produce a variety of deficits in aversive behaviour. Spiegel, Milner and Oppenheimer (1940) and Bard and Mountcastle (1948) report that rage may be released in cats with extensive damage to the amygdala and adjacent structures. Most investigators, however, have demonstrated a decrease in angry and fear behaviour after amygdalectomy (Rosvold, Mirsky and Pribram 1954; Kennard 1955/1956; Schreiner and Kling 1956; Woods 1956; Fuller, Rosvold and Pribram 1957; Wood 1958). Similar changes have been described in man (Terzian and Dalle Ore 1955). Masserman and his associates (1958) have recently reported that lesions of the amygdaloid complex produce mild or almost complete amelioration of neurotic behaviour in adult cats and monkeys respectively.

This report presents the results of lesions of the amygdaloid complex upon the defensive CRs and some components of experimentally induced neurotic behaviour in dogs.

MATERIAL AND METHODS

Six adult male dogs, D-8, D-9, D-10, D-15, D-20 and D-21, served as experimental animals. Three of them, D-8, D-9 and D-10 were trained in classical defensive CRs (type I), three others, D-15, D-20 and D-21, in avoidance (CRs type II). The dogs, exept for D-9 and D-10, were already used in other experiments and described elsewhere (Fonberg 1953; Brutkowski, Fonberg and Mempel 1960).

The animals were tested in a Pavlovian frame in a sound-proof conditioned-reflex chamber.

C l a s s i c a l - d e f e n s i v e CR (CR type I). In these experiments CS was reinforced by a single condenser discharge of 2μF and 90 V applied to the right hind leg. After about 100 trials CR was established: the animal lifted his leg and held it flexed until the noxious stimulus (UCS) was presented. The electric shock followed the CS after a 10-second delay and usually produced an increased flexion, accompanied frequently by a single scream. The experiments were continued for two more weeks using about 10 trials a day. Occasionally, intertrial CRs were noted.

A v o i d a n c e r e s p o n s e (C R t y p e II). The animal was trained to place his leg on a small board to avoid the electric shock whenever CS occurred. During the initial training the CS was either followed by a shock or by passive place-ment of the dog's leg in which case the shock was not applied. These two types of training trials occurred at random. With time the animal responded to CS by active avoiding the reinforcement. The avoidance response, which occurred in 100% of performances after being established, had been firmly fixed during a year-long training for another investigation (F o n b e r g 1958). The animals received about 10 trials per day separated by one-minute intervals. During testing many intertrial responses were also observed.

O p e r a t i o n s a n d H i s t o l o g i c a l e x a m i n a t i o n. After the pre-operative training had been completed, the animals were subjected to a two-stage amygdalectomy under Nembutal anesthesia. Lesions were made by suction under sterile conditions as described previously (B r u t k o w s k i , F o n b e r g and M e m p e l 1960).

The dogs recovered rapidly except for D-8 that stopped taking food spontane-ously for five months (B r u t k o w s k i , F o n b e r g , K r e i n e r , M e m p e l and S y c h o w a 1962).

In D-9, D-10, D-15, D-20 and D-21 lateral and ventral portions of the amygdaloid complex were removed bilaterally. In D-8 the lesion was extended into the depth of the amygdaloid complex and a complete destruction of the entire group of these nuclei was achieved. In addition, the latter lesion involved the antero-ventral tip of the Ammon's horn, the posterior part of the substantia innominata, the pyriform cortex along the ventral surface of the amygdaloid nucleus and a narrow strip of the adjacent neocortex on the right side. On the left side, the lesion was more extensive and involved also the caudal part of the olfactory tubercle, the postero-ventral putamen and almost the entire globus pallidus and substantia innominata. Additionally, the internal capsule was invaded at a few points.

RESULTS

C l a s s i c a l - d e f e n s i v e C R f o l l o w i n g a m y g d a l e c t o-m y. The effects of amygdalectomy on retention of this CR are presented in Fig. 1. As shown there, in the initial postoperative experiments the CR was completely abolished. However, it subsequently recovered and then was performed at the preoperative level.

The response to the UCS was also diminished in the immediate postoperative period. In addition, the number of intertrial CRs, which
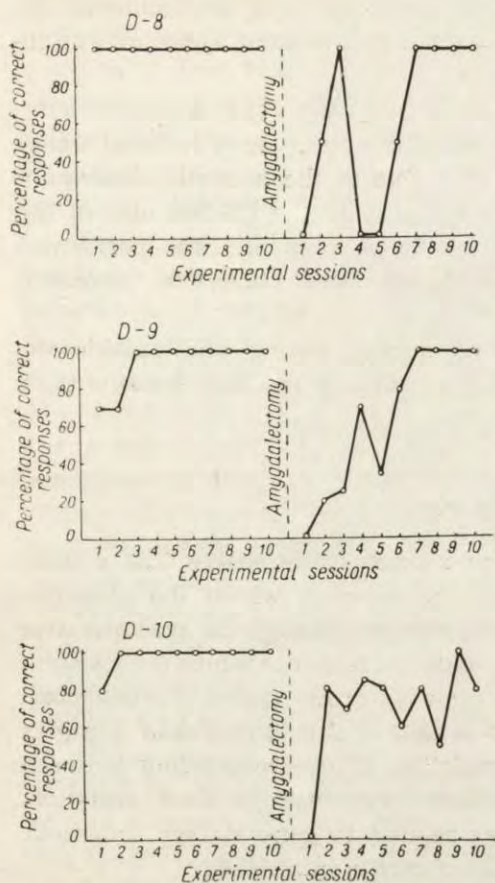
Fig. 1. Graph illustrating abolition of the classical defensive CR (type I) after amygdalectomy in the initial postoperative period.

Experimental sessions, comprising each 10 trials, marked on abscissa, while percentage of correct CRs is plotted on ordinate. See text.
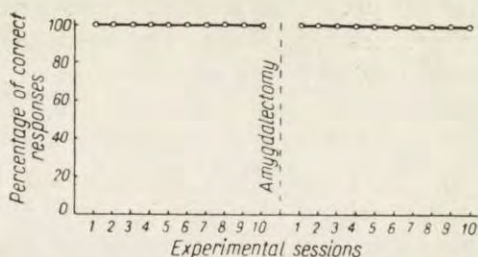
Fig. 2. Graph illustrating no effect of amygdalectomy upon avoidance response. The negative result was obtained in all three dogs tested (D-15, D-20 and D-21). See text.

Experimental sessions, comprising each 10 trials, marked on abscissa, while percentage of correct avoidance responses is plotted on ordinate.
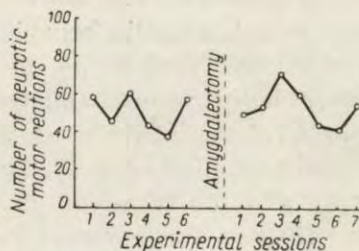
Fig. 3. Graph illustrating the number of neurotic motor reactions in D-15 before and after amygdalectomy.

could serve as an indication of the general fear behaviour in the experimental situation, was morkedly reduced after amygdalectomy. D-10 displayed an approach response towards food presented immediately after testing the defensive CRs. Before the operation this dog refused to take food under these conditions.

Avoidance behaviour following amygdalectomy. The results are summarized in Fig. 2. No impairment in performance on avoidance was noted in any of the three dogs. The response followed

every presentation of CS, was present from the very beginning of the postoperative testing, and remained unchanged without signs of extinction during 3 to 4 months of observation.

Effect of amygdalectomy on neurotic behaviour. In two dogs, D-15 and D-20, experimental neuroses were induced under stress preoperatively (F o n b e r g 1958). One of the neurotic abnormalities consisted of excessive responding not only to the CS but also in the intertrial intervals. In addition, the avoidance response was performed in food situation. Following amygdalectomy this behaviour remained unchanged (Fig. 3).

Continuous viewing of the animals during testing and outside the experimental situation indicated that after surgery the dogs became tame and placid.

DISCUSSION

Among the amygdalectomized dogs trained in defensive CRs a postoperative impairment was noted only in those in which the classical-defensive technique was used. There was no change in postoperative performance of the well-established avoidance response which is consistent with the result reported by B r a d y and his group (1954). Furthermore, the data presented suggest that the lesion of the amygdaloid complex did not affect neurotic behaviour consisting of overresponding between the trials and performing the avoidance response in food situation. However, both the intertrial responses related to general fear behaviour and the UCR to electric shock were temporarily diminished.

The dissociation between the postoperative maintenance of avoidance response and the transient impairment of the classical-defensive CR is rather difficult to reconcile. It may be possible, however, that it was due to unequal drive levels involved in both kinds of behaviour in our dogs. Whereas the classical response w a s certainly associated with fear since the CS was followed by a noxious reinforcement and the response was not overtrained, the avoidance response could get automatized with long preoperative training and, thereby, it did not necessarily take place at a high level of anxiety (Cf. A u l e y t n e r and B r u t k o w s k i 1960). The mechanism of the avoidance response and the role of fear in it is still an open question (S o ł t y s i k and K o w a l s k a 1960; S o ł t y s i k 1960 a, 1960 b). However, the data reported by S o l o m o n and his co-workers (1953 a, 1953 b, 1956) indicate that emotional reactions tend to d e c l i n e gradually during the avoidance training, and in some animals they disappear completely. Moreover, the authors found that avoidance response could be easily induced due to its "habit

strenght". Further, C o o n s has recently found that an avoidance response can be successfully trained when fear is r e d u c e d pharmacologically. Due to this evidence it may be assumed that an overtrained avoidance response, which was present in this investigation, does not reflect the fear behaviour as well as the classical-defensive CR or a non-firmly-fixed avoidance response (A u l e y t n e r and B r u t- k o w s k i 1960) .

If now, according to the findings that lesions in the amygdaloid region result in loss of shyness and ferocity as well as in reduction of fear behaviour, an impairment in defensive CRs following amygdalectomy could be expected, the classical and the non-firmly-fixed avoidance responses should be primarily affected, i. e. responses which were associated with a high level of fear. This conclusion was confirmed by the present observations of temporary decrement in the postoperative maintenance of classical-defensive CR and by that of W e i s k r a n t z (1956) who reported that an avoidance response, which had not been well established prior to operation, showed a more rapid extinction after amygdalectomy.

Furthermore, the different effects of amygdalectomy upon the classical-defensive CR and the avoidance behaviour suggest an involvement of brain structures selectively related to either of them. This is supported by R o b e r t s' demonstration (1958) "that animals will learn promptly to escape rapidly from an apparently strong noxious motivational state elicited by hypothalamic stimulation, without showing any avoidance of the stimulation in as many as 270 trials". It is likely then that also the amygdaloid region contributes to only one of these responses.

A final comment should be made on the neurotic motor reactions of two of our dogs. Although they were related to the defensive behaviour initially, it is possible that they lost their fear components subsequently and, similarly to the well-established avoidance response, remained unaffected after amygdalectomy.

SUMMARY

1. Three adult dogs were trained in classical-defensive CRs (type I) and three others in avoidance (CRs type II). The classical response was not well established, whereas the avoidance response was overtrained. In two animals of the avoidance group neurotic motor reactions were induced under stress.

2. All six animals were subjected to bilateral, two-stage resections of the amygdaloid complex.

3. Decrement in postoperative performance was restricted to classical-

defensive CR. Immediately after amygdalectomy CR was abolished completely. Subsequently, it recovered and was performed at the pre-operative level.

4. The well-established avoidance response remained unaffected after amygdalectomy.

5. The neurotic motor reactions were not abolished after amygdalectomy.

6. It is concluded that the amygdaloid complex is associated with defensive responses which are executed at a high level of fear.

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THE EFFECTS OF LESIONS OF THE MEDIAL HYPOTHALAMUS ON THE CONDITIONED REFLEXES TYPE II AND EMOTIONAL BEHAVIOUR

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It has recently been demonstrated (Hetherington and Ranson 1942, Brobeck 1946, Anand and Brobeck 1951 a, 1951 b, Anand, Dua and Shoenberg 1955, and others) that after damage to the medial hypothalamus hyperphagia occurs. Ever since this hypothalamic structure has been considered a "satiation centre" in contrast to the later discovered "feeding centre" which has been suggested to be localized in the lateral hypothalamus.

In addition to the above findings a few investigators have noticed changes in fear and angry behaviour following lesions of the medial hypothalamus. While using the electrical stimulation of the hypothalamus in cat, Hess and his associates (1949) have found a variety of emotional alterations. In many instances escape reactions could be elicited. At times, marked irritability as well as rage and aggression were observed. Increase in the defensive behaviour was produced only on stimulation of the posterior hypothalamus and the substantia grisea. Rage and aggression, which were obtained during the stimulation of the postero-lateral hypothalamus, were associated with all their manifestations — pilo-erection, extrusion of the claws, growling, snarling and crying together with dilatation of the pupils, biting and scratching objects. More recently Nakao (1958) described aggressive behaviour during stimulation of the central and the ventral portions of the medial hypothalamus. In an earlier study Wheatley (1944) has shown that damage to the medial hypothalamus in cat results both in hyperphagia and rage. The latter symptom was manifested both in response to man and animals. Also

P a p e z (1937) has regarded the hypothalamus as an important component of the proposed circuit of the emotional mechanisms.

The purpose of the present experiment is to study the effects of the lesions of the medial hypothalamus on the alimentary and defensive CRs in a hope to obtain a more detailed picture of the functional relations in this part of the diencephalon.

MATERIAL AND METHODS

Experiments were carried out on 15 male and female rabbits, aged from 2 to 3 years, which had preoperatively been trained in alimentary and defensive CRs type II (K o n o r s k i and M i l l e r 1933).

The training of these two responses was performed in two different experimental situations. Alimentary CRs were established in a box measured $1 \times 0,5 \times 0,5$ m. The front wall consisted of a glass permitting to watch the animal. Inside the box, at the right wall a small foodtray was placed. It contained 10 cups which were presented successively.

The box in which the training of the defensive CRs was carried out was a cube $1 \times 1 \times 1$ m. In the front wall a glass was also inserted. The floor was a mesh by means of which the electric shock was delivered if necessary. During the preliminary training procedure, in which the avoidance response was established, the voltage ranged from 30 to 70 V depending on the specimen. In the back of the box, at the left corner a horizontal bakelite triangular platform was fixed. It was placed 5 cm. above the floor and by a special device could be turned vertically to throw off the animal if it continued to stay there.

The following experimental procedure was used:

I. At first, the alimentary CR was trained. The animal was taught to place its right fore-limb on the foodtray, and this response was rewarded. No positive CS was used. The CR was displayed to the entire experimental situation. The reward was a small piece of carrot. The animal was permitted to eat ad libitum. Outside the testing cage the animal was given a determined amount of oats, hay and potatos. The inhibitory (negative or unreinforced) CS was the sound of a metronome (M) which was used once a day for one minute. When the animal refused to take food, the experimental session was discontinued. Thus, the number and the frequency of responses, as well as the amount of food taken during testing were determined by the animal. The rabbits were trained to a criterion of 10 correct inhibitory CRs in 10 consecutive experimental sessions.

II. Thereafter, in a different experimental situation the avoidance response was trained. The response was jumping on the bakelite platform whenever the positive CS, a whistle (W) was used. This response was never followed by shock. If the animal failed to jump on the platform, it was reinforced. The inhibitory (negative) CS was a buzzer (B). In the early period of training the animal jumped in response to B in the same way as it did to W. However, after a lapse of time the animal did not respond to B and continued to stay on the floor during the five-second presentation of this CS. B was never reinforced. Six positive and two inhibitory trials were randomly presented daily. The intertrial intervals were

1—3 minutes. All animals were trained to a criterion of 10 correct inhibitory CRs in 10 consecutive experimental sessions.

III. The training of defensive CRs was followed by a second series of alimentary CRs. On the third experimental day of this series, after a number of food presentations the positive defensive CS, whistle, was used. A few days later the animals were starved for 6 hours and, thereafter, while testing them W was used again to test whether or not there is a difference in response to the defensive CS after an increase in the alimentary excitability.

After the completion of training in conditioning, the animals were subjected to destruction of the medial hypothalamus under sterile conditions and nembutal anaesthesia (40 mg./kg. intravenously).

The operation was carried out in the Horsley-Clarke (Clarke, 1939) stereotaxic instrument with the headholder for rabbits described by Sawyer, Everett and Green (1954). After the incision of skin in the midline of the head two small openings in the skull were made 1 mm. apart of the saggittal suture and 2 mm. anterior to the coronal suture. Thereafter, two unipolar electrodes were vertically inserted in the brain at a level of 14 mm. below the surface of the skull and the tissue was coagulated with a constant current of 15 mA for 15 seconds.

After the operation the experiments were resumed and they were carried out in the same way and in the same sequence as before, but all three series were considerably shortened. After the postoperative training had been completed, the animals were sacrificed, and the location of the destruction was histologically verified.

RESULTS

Immediately after operation hyperphagia occurred in 9 animals. The rabbits ate faster and more vigorously and they gained on weight postoperatively. The food intake increased gradually until it achieved the level 2—3 times as high as before surgery. Due to the fact that under the described experimental conditions the food intake was determined by the performance of CR, the number and frequency of responses increased, and the entire experimental session was prolonged. Whereas before operation the animals ate for 20—30 minutes ad libitum, after surgery they took food for 60—180 minutes. The inhibitory CR was partially impaired, i.e. the animals often responded positively in the inhibitory trials.

Besides hyperphagia dramatic changes in the defensive behaviour of animals was observed. In this respect the animals may be classified in 3 groups:

I. Rabbits Nos. R-1, R-3, R-6

These three animals became tame and placid postoperatively. The defensive CRs declined, or they were absent in the first trials. The latent period of the avoidance response considerably increased. Whereas pre-

operatively the CR followed immediately the CS, after surgery it was delayed to 3 seconds in average. Escape response was also delayed. Whereas before operation the animals stayed on the platform after performance of the avoidance response and had to be thrown off from there, after operation they immediately left the platform and moved around on the floor. The inhibitory CR to B remained unchanged: the animals neither climbed the platform nor displayed any irritability. When the defensive CS, W, was applied in the alimentary situation, the response to it was strikingly diminished. Whereas before operation the animals exhibited a strong defensive reaction under these conditions, which was manifested in running away to a side or corner of the cage, panting, and refusing to take food for several minutes, after operation

Fig. 1. Frontal sections through the brain of rabbit No. R-1. The arrows indicate the sites of lesions.

the defensive CS elicited only an orientation reaction without any changes in emotional behaviour and any disorder in food intake.

Two months following hypothalamic destruction both hyperphagia and changes in defensive behaviour subsided.

The histological analysis revealed that lesion was placed in the central or dorsal portions of the medial hypothalamus (Fig. 1).

II. Rabbit No. R-2

After operation an increase in defensive CRs was noticed in this animal: the latency was shortened, the number of the intertrial responses increased and the inhibitory CR was completely disinhibited. The changes in CRs were accompanied by a considerable increase in general emotionality. The avoidance response was violent, so that very often the animal hit into the wall of the cage. Throwing off the animal from the platform

was often quite impossible. At intervals the animal was restless and often defecated. The defensive CS used in the alimentary situation elicited a violent locomotor reaction: the animal jumped back from the foodtray, ran away to side and became immobile for a few minutes. If it was provoked to move around and take food, it continued to crouch for half an hour or more. In consequence, the animal refused taking food in the experimental situation for 2—3 days. The defensive reactivity also

Fig. 2. Frontal sections through the brain of rabbit No. R-2. The arrows indicate the sites of lesions.

increased outside the testing box. The animal was very sensitive to touch stimuli and ran away when approached.

After one month the animal recovered, and there were no more changes observed either in the alimentary or in the defensive situations.

The histological control showed that the lesion was placed in the ventral part of the medial hypothalamus near the pituitary gland (Fig. 2).

III. Rabbits Nos. R-4, R-5, R-7, R-8, R-9

In contrast to the animals belonging to the preceding groups, in these five animals hyperphagia was accompanied by a pronounced aggressive behaviour. The animals tended to attack when approached, tried to bite and scratch the threatening hand or object. They also cried and snarled. When touched, they jerked away and when taken away from the cage, they resisted. The positive defensive CRs were not changed, while the inhibitory CR was occasionally impaired in the first postoperative trials. When the defensive CS was applied in the alimentary situation, the animals stopped eating for 3—5 seconds, but they did not run away. As soon as the defensive CS was off, the animal continued to respond to the alimentary CS and to take food. The rage outbursts were also noted outside the experimental situation.

Two-three months after operation both hyperphagia and aggressiveness subsided.

The histological analysis revealed that in all these animals the dorsal portion of the medial hypothalamus was damaged (Fig. 3).

In six remaining animals no changes were found after operation

Fig. 3. Frontal sections through the brain of rabbit No. R-7. The arrows indicate the sites of lesions.

either in alimentary or in defensive behaviour. Histologically, it was shown that the lateral part of the medial hypothalamus was demaged in them.

DISCUSSION

The above data indicate that after damage to the medial hypothalamus, in addition to an increase in food intake, a variety of other changes in emotionality occurs.

So far, the numerous investigations on the functions of the medial hypothalamus have shown that only lesions of the ventral portion of this area result in hyperphagia. However, the present study has indicated that any destruction of the medial hypothalamus, placed as far as 1 mm. of the third ventricle (Figs. 1, 2, 3), produces hyperphagia. Owing to this finding it is likely that the "satiation centre" located by A n a n d and B r o b e c k (1951 b) in the ventral part of the medial hypothalamus involves also other structures of the medial hypothalamus along the third

ventricle. It is to emphasize that changes in the fearlike and angry behaviour in rabbits are closely associated with the postoperative evolution of hyperphagia. On the other hand, lesions of the hypothalamus, which do not produce any increase in food intake, fail to alter the animal's emotionality. Histological verification has shown that the postoperative changes in the defensive CRs and aggressiveness result from lesions of the medial hypothalamus. In particular, the aggressive behaviour was produced by lesions of the dorsal part of the medial hypothalamus (Fig. 3) indicating that in this area the "centre of suppression of aggressiveness" is located. In this connection it is worth mentioning — according to the N a k a o's (1958) results — that aggression in cat is elicited by stimulation of the ventral and central portions of the medial hypothalamus.

On the basis of the described results it may be assumed that the entire medial nucleus of the hypothalamus exerts a moderatory influence on food intake while only small areas of this nucleus are concerned with suppression of the defensive or aggressive responses. It seems likely that in the ventromedial hypothalamus the "aggression centre", and in the dorsomedial hypothalamus the "fear centre" can be located. It can be further hypothesized that between these two "centres" antagonistic relations exist. Due to this suggestion all changes in emotional behaviour in rabbit can be ascribed to lesions of either of these "centres" or both of them. It is likely that they partially overlap because pure symptoms can be obtained only after damage to restricted areas. It is possible that the postoperative aggressiveness was produced by lesions of the "fear centre" while the postoperative fear increase resulted from lesions of the "aggression centre" situated in the lower parts of the medial hypothalamus. A postoperative diminution of defensive behaviour could be associated with partial lesions of both "centres" (Fig. 1).

The fact that the postoperative changes subside and the animals recover in the late postoperative period indicates that there are other brain structures which — in addition to the medial hypothalamus — moderate the food intake and exert suppressive influence on some other aspects of the emotional behaviour. This assumption gains support in a number of recent evidences showing that hyperphagia or rage can be elicited on electrical stimulation or produced by lesions of certain paleocortical or mesocortical structures (A n a n d, D u a and C h h i n a 1958, M o r g a n e and K o s m a n 1957, 1960, M a c L e a n 1955, R o s v o l d, M i r s k y and P r i b r a m 1957, B r u t k o w s k i, F o n b e r g and M e m p e l 1961, F u l l e r, R o s v o l d and P r i b r a m 1957).

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SUMMARY

The purpose of the present paper was to study the effect of lesions of the medial hypothalamus on defensive and alimentary CRs type II together with general emotionality in rabbits.

The following results were obtained:

1. An increase in food intake is produced not only by lesions of the ventral part of the medial nucleus of the hypothalamus, but also by the destruction of other areas of this nucleus situated close to the third ventricle.

2. The lesions of the medial hypothalamus which result in an increase in food intake and alimentary CRs produce also changes in defensive CRs and emotionality.

3. The destruction of the dorsal portion of the medial hypothalamus produces aggression and rage attacks.

4. The destruction of the ventral portion of the medial hypothalamus produces an increase in defensive CRs and in the general defensive behaviour.

5. The destruction of the central portion of the medial hypothalamus produces a diminution of defensive CRs and of the general defensive behaviour.

6. All changes in conditioning and general behaviour subside 1—3 months after operation.

7. Both aggressive behaviour and changes in defensive conditioning occur along with hyperphagia and subside when hyperphagia disappears.

8. The destruction of the lateral portion of the medial hypothalamus does not produce any changes either in food intake or in emotionality.

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A THREE-DIMENSIONAL MODEL OF THE STRIATAL NUCLEI IN THE DOG'S BRAIN

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The growing interest for the experiment on the striatal nuclei makes it necessary to have an adequate knowledge of the real shape of these structures in laboratory animals. Nevertheless, except for some atlasses of sections (for dog's brain A d r i a n o v and M e r i n g 1959 and L i m, L i u and M o f f i t 1960, for cat J a s p e r and M a r s a n 1954, for rat C r a i g i e 1925 and G u r d i j a n 1928, for rabbit W h a r t o n Y o u n g 1936), and a few reconstructions of the human brain (e.g. K l i n g e r 1942, K r i e g 1957 and N e t t e r 1959) it is rather difficult to find papers on this topic in the literature. This paper is intended to fill up this gap by furnishing the description of a three-dimensional wax model of the striatal nuclei in dog.

The basis for the construction of our model was provided by an uninterrupted series of dog's brain, fixed in formalin, embedded in paraffin and cut in the frontal plane. The sections were 20 μ thick, stained alternately according to the methods of Klüver-Barrera and Nissl. Every 25th section was drawn with the help of a projector in a 10 times magnification on a 5 mm. plate made of a mixture of paraffin and beeswax, and the contours of the striatal nuclei were cut out. Five uninterrupted series of dog's brains, cut in three basic planes and stained according to the methods of Weigert, Nissl and Klüver-Barrera resp. were used for comparison and control of the model.

A special attention was paid to the topographical situation of the striatal nuclei in relation to the surface of the brain. For this sake, a projection of the striatal nuclei was made on the lateral and medial aspect of the brain (Figs. 5, 7). The model was used also to determine the volume of the particular nuclei of the brain modelled. The models were weighed and the volume calculated from the specific

weight of the substance used for modelling. Therefore the data are relevant only for the modelled brain and have a relative value.

According to most handbooks the striatum comprises the caudate nucleus, putamen, nucleus accumbens, globus pallidus, amygdaloid complex and claustrum. In our model claustrum has been omitted, since it was described in a separate paper (T e n e r o w i c z 1961).

The caudate nucleus

The caudate nucleus is the largest of the striatal nuclei. In the dog it has the shape of an irregular clad, rather difficult to describe (Figs. 1—4 Caud.). Its medio-lateral dimension in the brain modelled is about 5.6 mm; the oro-caudal dimension measured in the middle, amounts to about 7.3 mm. The largest dimension is that from the dorso-caudal to the oro-ventral point. It is about 14.2 mm.

We can distinguish a medial, lateral and oral surface in the caudate nucleus. The medial surface (Fig. 1) is smooth. It immediately touches the lateral ventricle. Its ventral portion is situated almost vertically
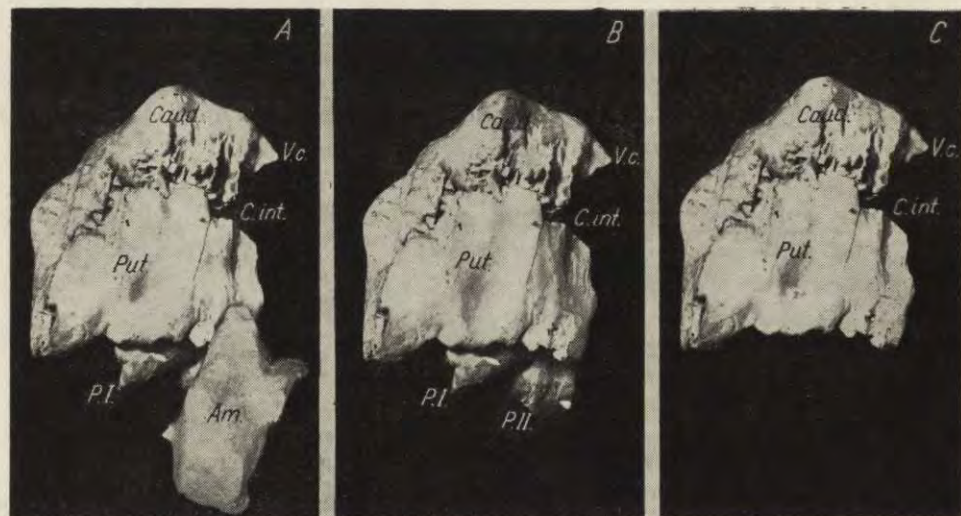
Fig. 1. Medial view of the model of the striatal nuclei in the left hemisphere of the dog's brain.

A — all striatal ganglia "in situ"; B — the same, amygdaloid complex and nucleus accumbens removed; C — caudato-putamen after removal of pallidal nuclei. Abbreviations: Acc. — nucleus accumbens; Am. — the amygdaloid complex; C. int. — the internal capsule; Caud. — caudate nucleus; Opt. — the optic tract; Pal. I — pallidum I; Pal. II. — pallidum II; Put. — putamen; V.c. — vestige of cauda nuclei caudati.
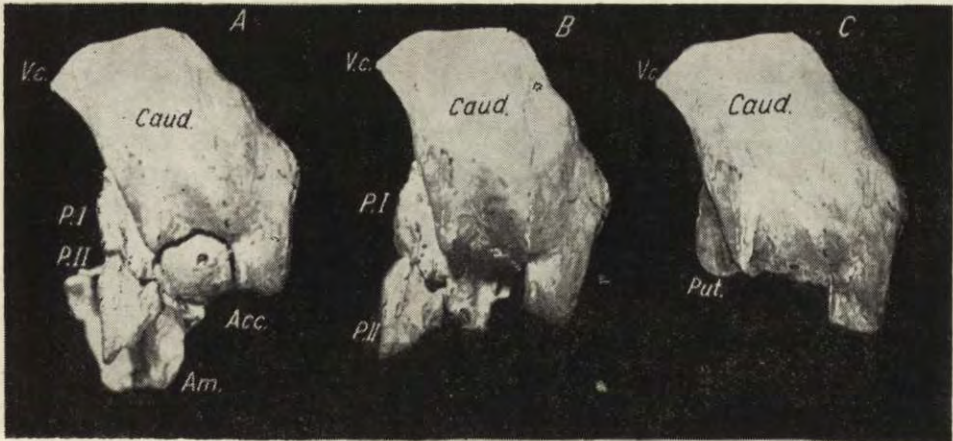
Fig. 2. Lateral view of the model of the striatal nuclei in the left hemisphere of the dog's brain Labellings see Fig. 1.
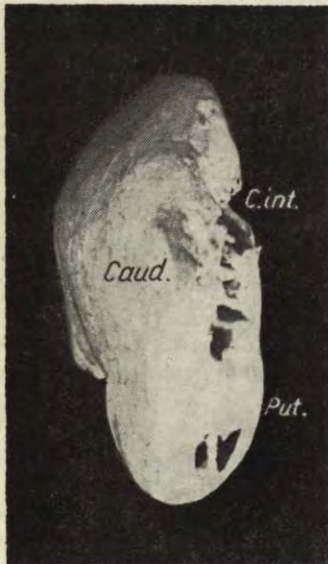

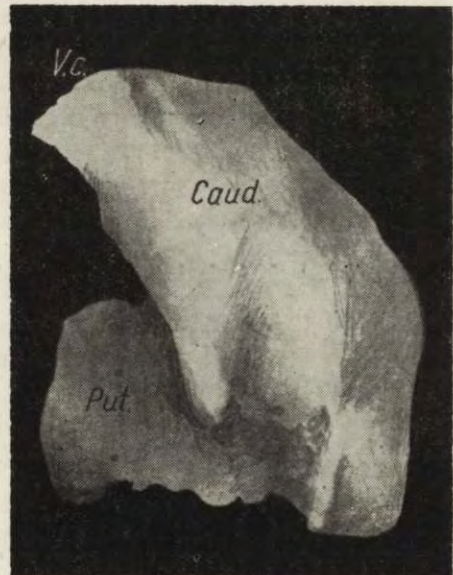Fig. 3. Oral view of the caudato-putamen.

Fig. 4. Model of the caudato-putamen seen from a medio-caudal aspect.

and shows a slight bulk in the middle. The upper part is inclined dorso-laterally and, in the back portion, also caudo-laterally (Fig. 3). In the dorsocaudal top of the nucleus a small appendix is seen, resembling a cone flattened medio-laterally (Figs. 1, 2, 4 V.c.). This is the vestige of the cauda nuclei caudati, which in the dog appears only in such a reduced form. The elongated cauda reaching the amygdala, as describ-ed by B r a d l e y (1959) has never been found by us in any of our series of dog's brains.

The dorsal portion of the caudate nucleus has the shape of a blunt wedge. The anterior ridge (Fig. 4) is formed similarly. Only ventrally a wider basis is found where the caudate nucleus touches the basal structures of the telencephalon usually called substantia innominata. It is rather difficult to draw the boundaries of the caudate in this area.

The medial surface of the caudate (Figs. 2, 3) is very rough in con-trast to the lateral surface. It is formed by the bundles of the internal capsula. The internal capsule of this region consists of numerous bundles running rather independently one from another. Many of them press into the mass of the caudate, or perforate it, thus causing the gray mat-ter of the nucleus to be spongy or to form many thornlike excrescences. Many of these excrescences, especially in the anterior portion, perfo-rate the internal capsule and thus form many small bridges of the gray matter (Fig. 2) connecting the caudate nucleus with the putamen. Their number increases when observed more oro-ventrally, and finally the bases of both nuclear masses coalesce. This coalescence is perforated here only by the bundles of the anterior commissure. In the ventral part of the caudate an incision is seen here (Fig. 4). This is the room for the nucleus accumbens described below.

Quite different from the rough plane of the contact between the caudate and the internal capsule is the upper part of the medial surface of the caudate nucleus. The caudate touches here the compact mass of fibers of the semioval centre. This part of surface is almost perfectly smooth. Moreover, it is a continuation of the smooth lateral surface of the putamen (Figs. 1, 3). This fact supports the term "caudato-putamen" introduced by some authors. This structure may be considered as a uni-form mass perforated by the fibers of the internal capsule and divided by it into the lateral putamen and medial caudate.

When projected on the lateral surface of the brain (Fig. 5A), the caudate nucleus appears under the anterior sylvian and anterior ectosyl-vian gyri, extending also under the back part of the anterior composite gyrus and orbital gyrus. Ventrally it intrudes into a portion of the piri-form gyrus. On the medial aspect of the hemisphere (Fig. 5B) the out-lines of the caudate comprise the anterior part of the corpus callosum
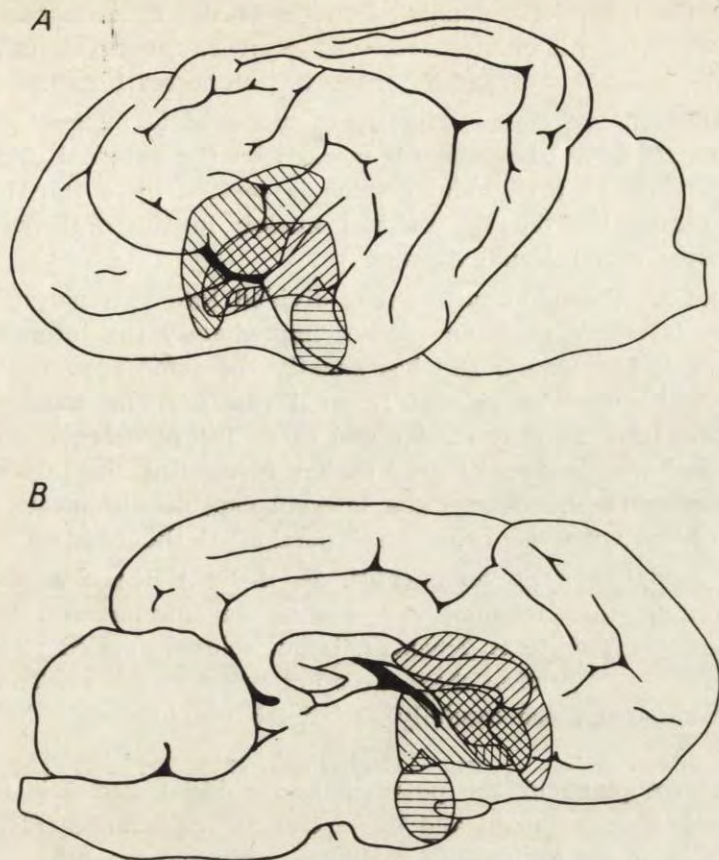
A

B

Fig. 5. Topographical situation of the caudato-putamen, accumbens and amygdaloid complex.

A — a projection on the lateral aspect of the brain, B — a projection on the medial aspect of the brain.

and an adjacent portion of the anterior cingular gyrus, septum pellucidum, subcallosal gyrus, and a part of the subgenual area.

The volume of the caudate was determined together with putamen since both these nuclei cannot be separated. Their joint volume in our dog was about 295.0 mm³. making about 63.5% of the total volume of the striatal nuclei modelled.

Putamen

The putamen in the dog (Figs. 1—4 Put.) is a flat body, about 1,7 mm. thick. Its silhouette slightly resembles that of a rough semicircle. Its contour, however, is zigzag-like, especially in the dorsal parts. This is

caused by the irregularly running bundles of the internal capsule. The dimensions of the putamen in our dog are: oro-caudal about 9.2 mm., dorso-ventral on the average 5.2 mm., the highest 7.1 mm.

The putamen is situated laterally to the caudate nucleus and internal capsule. Its lateral boundary is marked by the external capsule. The medial boundary in the caudal portion is formed by a thin medullary lamina dividing it from the pallidal nuclei; in the oral portion this lamina passes into internal capsule.

The medial surface of putamen is divided into two parts. The oro-dorsal part is where putamen touches immediately the intenal capsule. The surface is here rough and has exactly the same appearance as the caudate on the opposite side of internal capsule. The bundles of the capsule press into the gray matter and cause the occurrence of peculiar processes and fine bridges of gray matter connecting the putamen with caudate. Orally the bundles of the internal capsule disappear, and thus putamen unites with the oro-ventral portion of the caudate.

In its caudal part putamen (Figs. 2c, 4 Put.) lies close by to the globus pallidus, thus forming the nucleus lentiformis well known in human anatomy. This term, however, is but seldom applied to the brain of carnivores, as its general shape does not resemble a lens. The pallidal nuclei are situated more caudally and touch putamen only on a small area.

The contact plane of the putamen and pallidal nuclei is found on the caudal part of putamen and has a smooth appearance (Fig. 4). The nuclei closely touch each other, pallidum only by the oral portion of its lateral surface. They are separated by a thin lamina of medullated fibers. The lateral surface of putamen is smooth.

As putamen is a flat mass lying between the internal and external capsule the edges of this nucleus are rather sharp. The caudal border is most interesting. Putamen penetrates here between the amygdaloid and pallidal nuclei, its limits being subject of a controversy. In most papers this region remains unlabelled... Our concept of delimitation is based on myeloarchitectonics and will form the subject of a more detailed analysis.

Topographically the putamen is situated (Fig. 5) under the ventral portion of anterior and posterior sylviac gyri extending orally under the caudal portion of the orbital gyrus and a portion of the adjacent piriform cortex. Medially it is found behind the septum below the callosal commissure and behind the anterior part of the thalamus.

The volume of putamen was calculated together with that of the caudate nucleus.

Globus pallidus

For the brain of the dog the term "globus" is applied only by analogy with the human brain, as the pallidum of the dog does not resemble a globus. Its general lateral silhouette (Figs. 1a, 1b, 2a, 2b, PI, and PII) roughly resembles a triangle with its basis turned caudad. The ventral boundery of this triangle, however, is interrupted by a bulk projecting ventrad. The gap behind it is filled by the optic tract (not modelled).

Globus pallidus in the dog's brain consists of two parts separated by a thin medullary lamina. In their relation to each other the two parts are situated differently from those in man. Pallidum II (Fig. 6) occupies the ventro-caudal part of the whole, while the larger pallidum I takes the oro-dorsal position. The boundary between the two parts, marked by the medullary lamina has a complicated, peculiar shape. The upper and oral part of pallidum II intrudes, rather deeply, into the niche of pallidum I.

The dimensions of pallidum I are: oro-caudally in the middle 6,1 mm., dorso-ventrally about 5 mm. The thickness varies from 1 mm orally and dorso-caudally to 2,8 mm. in the middle. Respective data for pallidum II are: oro-caudally about 3,3 mm., dorso-ventrally about 4.4 mm. and medio-laterally 2,2 mm. Considered together, as situated in the brain, the pallidal nuclei are about 8,3 mm. dorso-ventrally in the hind part and 6.1 mm. oro-caudally.

The lateral surface of pallidum I touches the medial aspect of putamen, separated from it by the medullary lamina mentioned above. This surface is smooth and slightly convex. Ventrally pallidum reaches below the ventral edge of putamen and meets here the ventral part of the internal capsule. Pallidum II does not touch the putamen. Its smooth lateral surface touches the ventral portion of pallidum I and the optic tract.

The medial surface of the pallidal nuclei contacts with the internal capsule. In contrast to the rough surface of the medial aspect of putamen contacting the internal capsula, the surface of the pallidal nuclei appears here to be smooth with only a few shallow impressions. The dorsal edge of pallidum (only pallidum I) is rounded and delimited by bundles of centrum semiovale.

Topographically the pallidal nuclei (Fig. 7) are found under the ventral part of the posterior sylviac gyrus, a small adjacent portion of anterior sylviac gyrus and the piriform cortex. Seen from the medial aspect of the hemisphere, they are hidden behind the anterior part of thalamus and the ventral part of septum.
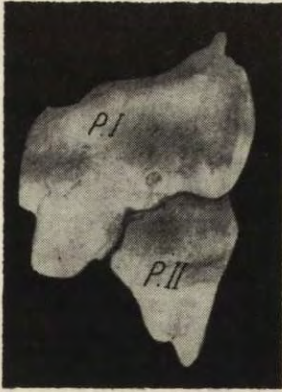
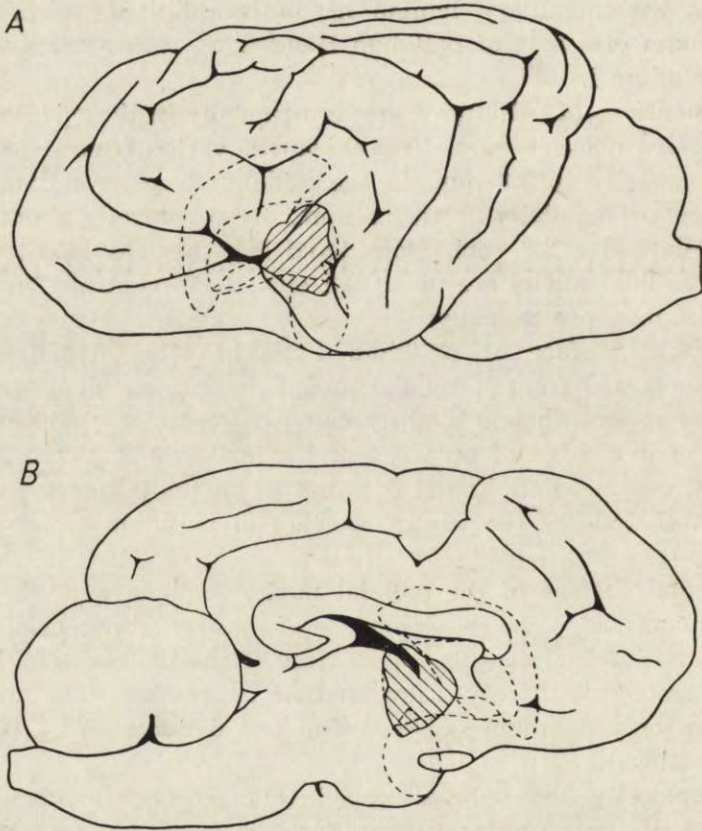Fig. 6. The model of pallidal nuclei. Lateral view.

Fig. 7. Topographical situation of the pallidal nuclei.

A — a projection on the lateral aspect of the brain, B — a projection on the medial aspect of the brain.

The volume of pallidum I is about 43.7 mm.³ making 9.4% of the total volume of striatal nuclei. The volume of the smaller pallidum II is about 19.5 mm.³ i.e. 4.2%.

Nucleus accumbens

Nucleus accumbens (Fig. 1 Acc.) is the smallest of the striatal nuclei. Its dimensions are: 3.4 mm., oro-caudally, and 4.9 mm. ventro-dorsally. It is a close continuation of the caudate nucleus and joins it closely filling a niche in the ventral part of caput (Fig. 4). Nevertheless, the boundaries are distinct when seen under the microscope, since the cells and myeloarchitectonics of both structures differ considerably.

The shape of the nucleus accumbens is roughly similar to a half of a convexo-concave lens with its base turned orad and the concavity turned laterad. The medial surface is smooth and touches the structures of septum. In the middle of the lateral surface there is a slight bulk dividing the surface into a dorsal and ventral portion. The dorsal portion meets immediately the lateral ventricle, the ventral touches the head of caudate nucleus. Nucleus accumbents is situated under the bottom of the lateral ventricle so that its upper part is found medially to it. Its volume in the brain modelled is about 14.7 mm.³, which makes 3.2% of the total weight.

The amygdaloid complex

The amygdaloid complex holds a special position among the striatal nuclei being situated a little aside (Figs. 1, 2 Am.) and more ventrally than the other nuclei. Its dimensions are: medio-laterally in the middle about 6.2 mm., dorso-ventrally about 7.4 mm., oro-caudally at the lateral surface 4 mm., at the medial 2.3 mm. When seen from behind (Fig. 8) it shows an approximately ovoidal silhouette, and from the dorsal side it is similar to a high trapezium the medial side being narrower than the lateral.

The boundaries of amygdala are still a matter of discussion and in some places cannot be precisely determined. The most definite limits are found at the lateral side where the amygdala is bordered by a thin lamina of white matter — capsula externa. Medially the amygdaloid complex touches the optic tract and the lateral aspect of pallidum. Medio-caudally the amygdaloid nuclei form the lateral wall of the lateral ventricle. The remaining surfaces are a subject of controversy. Orally, amygdala passes into the substantia innominata, and its exact

limits are here a matter of agreement. Ventrally and ventro-medially, the amygdaloid nuclei are bordered by cortical structures partially very reduced. The cortical nucleus making this part of amygdala is considered by some anatomists (e.g. Ad r i a n o v 1959) to be a part of the cortex. Dorsally amygdala touches the putamen, the boundary being vague, e.g. the most dorsal promontory of our model (Fig. 8) is regarded as

Fig. 8. The model of the amygdaloid nuclei seen from behind.

belonging to putamen, while we consider it as belonging to the amygdala basing on its myeloarchitectonics.

The surface of amygdala is mostly smooth. A small projection visible on the oral aspect (Fig. 1A) is made by the nucleus of the lateral olfactory tract. Another one, on the top (Fig. 8) is an anonymous nucleus bordering the lateral aspect of the putamen. A groove on the medial side is occupied by the stria terminalis. Finally a shallow impression on the lateral surface is due to the deep sylvian fissure.

Topographically amygdala occupies (Fig. 5) the most ventral part of the anterior sylviac gyrus and the adjacent piriform cortex extending caudad over the posterior lip of the sylvian fissure. Its volume in our dog is about 92 mm.^{3}, thus representing about 19.8% of the total mass of striatal nuclei.

SUMMARY

A three-dimensional beeswax model of the dog's striatal nuclei was used as a basis for description of the plastic shape of the caudate nucleus, putamen, nucleus accumbens, pallidum and amygdaloid complex. The outlines of these nuclei are projected on the medial and lateral aspects of the brain in order to show their situation in the brain.

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CONTENTS